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THE REPRODUCTIVE CYCLE, MOVEMENTS, AND PRE-NESTING BEHAVIOR OF ADULT AND YEARLING FEMALES IN A POPULATION OF BLUE GROUSE

by

(C) SUSAN J. HANNON

A THESIS

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ABSTRACT

Aspects of the reproductive cycle and pre-nesting behavior of female blue grouse (*Dendragapus obscurus fuliginosus*) were investigated on Vancouver Island, British Columbia, during the summers of 1976 and 1977. Emphasis was placed on comparison between adult and yearling hens.

Oviducts of yearlings recrudesce later, reach a lower laying size and regress faster than those of adults. Yearlings appear less sexually mature than adults, however are able to accelerate gonadal development in years when adult numbers are low.

Two groups of yearlings were identified: those which could potentially breed, termed *breeders*, and those unlikely to breed, termed *non-breeders*. Both groups of yearlings were present on the breeding range in April, but *non-breeders* disappeared soon after yearlings began to lay eggs. *Breeders* weighed more than *non-breeders* throughout the spring.

Reproductive status of live hens was determined by measuring total plasma calcium. Pre-laying hens in the slow phase of gonadal recrudescence could be distinguished from those in the rapid phase using this method, but the precise reproductive status could not be ascertained.

Yearlings move over longer distances and localize later than adults during the pre-nesting period. Site attachment

was a necessary prerequisite to gonadal development. Hens replied to an aggressive call (the cackle) during the pre-nesting period, primarily when they were localized and in the rapid phase of gonadal recrudescence. Hens may space themselves on the breeding range by mutual avoidance, using the cackle call.

A model is presented which relates the above information to a mechanism for regulating density of hens on the breeding range.

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INTRODUCTION

Current theory, based on over ten years of observations and experiments with blue grouse on Vancouver Island, indicates that the size of the breeding population is regulated on the summer range by the expulsion of yearlings of both sexes (Bendell et al. 1972, Zwickel 1972). Behavioral interactions between resident adult females and yearling female recruits may occur to establish numbers of females on the breeding range (Zwickel 1972). Thus, females may play an important role in determining numbers of birds in the breeding population.

This thesis investigates various aspects of the life history of female blue grouse, stressing comparisons between resident adults and recruiting yearlings. Differences between the two age classes may help to elucidate how recruitment is limited. The work is presented in the form of four papers:

1. Gonadal cycles of adult and yearling blue grouse.
2. Characteristics of non-breeding and breeding female blue grouse.
3. Plasma calcium as an indicator of reproductive condition in female blue grouse.
4. Behavior of female blue grouse during the pre-nesting period.

The first paper examines differences in the gonadal cycles of adults and yearlings and discusses general features of follicular development and regression in the species. In the second paper, yearlings collected as part of a removal experiment were identified as non-breeders and breeders when compared to known breeders. A comparison of the two groups enabled me to determine the timing of exclusion of recruits in spring and to discuss other factors which could cause certain yearlings to be excluded.

When studying live birds in the pre-nesting period, the reproductive status of the hen had been impossible to determine. The third paper discusses a method which separates hens in the slow phase of gonadal recrudescence from those in the rapid phase. The distinction had importance when assessing behavioral responses of hens.

Pre-nesting movements and the responses of hens to a taped aggressive call are examined in the fourth paper to determine how hens space themselves on the breeding range.

The results are integrated in a final discussion.

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Bendell, J. F., D. G. King, and D. H. Mossop. 1972. Removal and repopulation of blue grouse in a declining population. J. Wildl. Manage. 36: 1153-1165.

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PAPER 1. GONADAL CYCLES OF ADULT AND YEARLING BLUE GROUSE

Abstract

The gonadal cycles of adult and yearling female blue grouse (*Dendragapus obscurus fuliginosus*) collected from Vancouver Island, British Columbia, were studied. Gonadal cycles were similar to those of other periodic breeders. Yearling females recrudesce later, lay eggs at a lower oviduct weight, and regress faster to a lower oviduct weight than do adults. Yearlings appear to be less sexually mature than adults, but delays in or lack of breeding could be a result of social interaction with resident adults.

Introduction

Populations of blue grouse on Vancouver Island, British Columbia, have been studied extensively since 1950, primarily to determine how breeding numbers are regulated (Bendell 1955, Bendell and Elliott 1967, Zwickel and Bendell 1967, Zwickel 1972, Bendell et al. 1972, Zwickel 1975). A comprehensive study of the gonadal cycles of females and males has never been published. Since the yearling age class is the recruiting segment to the population in spring, differences between adult (>22 months) and yearling (10-14 months) birds may be of importance to population regulation.

Standing (1960), in an unpublished study of blue grouse (D. o. pallidus) in Washington State, presented data on the gonadal cycles of females. He stated that adults ovulated earlier than yearlings.

Differences have been noted between adult and yearling birds in Vancouver Island populations. Yearling females can breed, but have smaller clutch size (Zwickel 1975) and usually hatch eggs a week later than adults (Zwickel 1977). Both age classes have similar fertility and hatchability of eggs and equal nesting success (Zwickel 1975). Zwickel and Lance (1965) suggested that, unlike adults, yearlings are not as able to renest if their first clutch is destroyed.

The objective of this study is to present information

on the gonadal cycle of female blue grouse at macroscopic and histological levels, stressing differences between adults and yearlings.

Study Areas

Specimens were collected from 2 study areas, Tsolum Main and Upper Tsolum Main, located on the east slope of Vancouver Island, in a region west of Courtenay, British Columbia (Fig. 1). The general area is intermediate between the coastal Douglas fir (*Pseudotsuga menziesii*) and coastal western hemlock (*Tsuga heterophylla*) biogeoclimatic zones (Krajina 1965). Mature forest once covered the study areas; it was logged, burned at various times, and largely replanted with Douglas fir or allowed to regenerate naturally. For a more detailed description of the study areas see Zwickel and Bendell (1967), and Zwickel (1972, 1977).

Methods

Collection of hens

Most material for this study was collected during removal experiments on Tsolum Main. Almost all adult and yearling birds were shot between 17 May and 24 July 1970 (Zwickel 1972). From 1974 through 1976 yearlings only were collected from early April through 24 July. In 1976, adult and yearling hens were shot at Upper Tsolum Main from 26 April through 3 June to increase the spring sample size of adults and as a comparison to collections from Tsolum Main. A total of 69 adult and 198 yearling hens was removed. Material was also collected on 28, 29 August 1976 from 29 hens killed by hunters on or in the vicinity of the study areas.

Necropsy of hens

Necropsies were performed on most birds from the early collections (1970) and on all birds from later studies. Ovaries and oviducts were excised and placed in 10% formalin or Bouin's solution. These organs were weighed to 0.01 g after being blotted dry of preservative. If an egg was

present in the oviduct, the organ was weighed with and without the egg. The largest nonovulated follicle of each ovary was measured with vernier calipers to the nearest 0.01 mm, across the stigma at the widest point. In 10 samples which had an egg in the oviduct and 4 or less recent postovulatory follicles (ie. the hen was actively laying), the 12 largest developing follicles were measured. In all samples which had an egg in the uterus, the length of postovulatory follicles was measured from the base of the pedicle with vernier calipers. Samples which contained an oviducal egg were used in the above measurements to ensure that comparison was made among birds in the same stage of the laying cycle. The presence or absence of a brood patch was noted for each bird.

Counting postovulatory follicles

Postovulatory follicles were examined in the ovaries of 42 adult and 59 yearling hens to discover how long postovulatory follicles persist as easily identifiable structures, to compare number of ovulations in adults and yearlings, and to assess the extent of renesting in adult and yearling hens. Ovaries were chosen from the collection to span the laying and post-laying season. All ovaries from incubating hens were used but due to the secretiveness of hens at this time, the sample size was small (N=6). Almost

all 1970 (mainly adults) and 1976 (mainly yearlings) samples in which ovaries were intact were used. The best preserved samples were chosen. Ten ovaries (5 adult and 5 yearling) were examined from specimens shot by hunters.

All ovaries were inspected under a dissecting microscope for evidence of postovulatory follicles. Ovaries in which it was impossible to count postovulatory follicles macroscopically were embedded in paraffin, serially sectioned at 10 u, and stained by the Masson's Trichrome Method (Mallory 1938). From 55-100 sections were examined from each ovary, depending on its size, and postovulatory follicles counted. Postovulatory follicles were distinguished from burst atretic follicles and resorptive atretic follicles by the criteria described by Davis (1942), Payne (1966) and Erpino (1969). Of 101 ovaries examined, 65 required histological treatment.

General definitions and calculations

Hens were assigned to the following categories based on characteristics of their gonads and the presence or absence of brood: pre-laying (presence of preovulatory follicles, no postovulatory follicles); laying (presence of an oviducal egg or recent postovulatory follicles); incubating (no oviducal egg, mature follicles regressing); brood (females with brood, ovary regressed); and lone (females with no

brood, ovary regressed).

The age of juveniles accompanying hens was determined using molt and development of primary feathers (Zwickel and Lance 1966, Redfield and Zwickel 1976). The age of postovulatory follicles in ovaries of hens with brood was calculated by adding the modal age of the brood plus 26 days for incubation (Standing 1960).

Since samples were collected from different areas and over a number of years, I wished to determine if the data could be grouped. Date of hatch for all juveniles captured on Tsolum Main and Upper Tsolum Main was determined by subtracting the mean age of the brood from the capture date. Thus, the time of peak hatch (Zwickel 1977) was computed for different areas and years.

By arranging follicles in order of increasing diameter (preovulatory) or decreasing length (postovulatory) and taking the mean of each size class, a hypothetical curve for the development and regression of a single follicle was constructed. Since blue grouse lay one egg every 1.5 days (Standing 1960), the time before or after ovulation of each size class of follicle could be calculated. Date of laying first egg was calculated by counting the number of postovulatory follicles and backdating 1.5 days for each postovulatory follicle.

Total number of adult hens on Tsolum Main for several years was estimated using a marked-resighting equation (Redfield 1972, Zwickel unpublished data).

Weekly or biweekly means (data from some weeks were lumped due to low sample size) of weights of oviducts and diameters of the largest nonovulated follicles for yearlings and adults were calculated. Some follicles were damaged during handling or by shot penetration making the ovarian sample smaller than for oviducts. Mean number of postovulatory follicles, oviduct weight, and preovulatory follicle diameter during laying were tested for significant difference between adults and yearlings with an unpaired t-test.

Results

Female gonadal cycle

All years in which collections were made at Tsolum Main had a peak hatch period during the same 2 weeks (Zwickel 1975, unpublished data). Peak hatch for hens on Upper Tsolum Main was the same as that on Tsolum Main.

Fig. 2 traces the development and regression of a follicle in a blue grouse ovary. Follicles develop very slowly up to approximately 6 mm in diameter, after which a rapid development over a period of 9-10 days brings them to an ovulation size of approximately 30 mm in diameter. Postovulatory follicles regress quickly, reaching half their immediate postovulatory size within 4-5 days, then regress more slowly.

The mean diameter of the largest nonovulated follicle in the ovaries of adults and yearlings is plotted in Fig. 3. Follicles in yearling ovaries are initially smaller than those of adults but gain adult size during laying about 10 days later than adults. Follicles of both age classes regress rapidly at first and then more slowly. Follicles of yearlings are similar in size to those of adults during the slow regression phase.

Weekly or biweekly means of weights of oviducts are

plotted against time for adults and yearlings in Fig. 4. Oviducts of yearlings are initially lighter than those of adults, reach a smaller size during laying, and regress to a lower weight during July. In late August, ovaries and oviducts of adults taken from hens killed by hunters were heavier than those of yearlings and ovaries of yearlings were heavier than those of juveniles (Table 1). These differences were significant when tested with a one way analysis of variance and Duncan's multiple range test ($p<0.01$).

Laying adults were shown to lay over a longer time period, at a higher oviduct weight ($p<0.01$, unpaired t-test), but with follicles at the same diameter as yearlings (Table 2).

Oviducts of yearlings on Tsolum Main in 1976 appeared to be developing earlier than those of yearlings from Upper Tsolum Main in 1976 and yearlings collected in 1974 through 1975. To test this, the mean laying date of first egg for 1974-1976 for each area and age class was calculated by backdating from the number of postovulatory follicles in laying hens (Table 3). Mean laying date was not significantly different between adults on Upper Tsolum Main in 1976 and yearlings on Tsolum Main in 1976, whereas all other yearling groups laid 8-10 days later ($p<0.01$, one way analysis of variance, Duncan's multiple range test).

To test whether there was a relationship between numbers of adults and gonadal development in yearlings, I

compared peak hatch periods of adults and yearlings with total number of adults at Tsolum Main (Fig. 5). In the 2 years in which adult numbers were low (1971 and 1976), adult and yearling hens had the same 2 week peak hatch periods. This indicates that yearlings may be able to accelerate gonadal development when adult numbers are low.

Number of postovulatory follicles

The stages in regression of postovulatory follicles in the ovaries of blue grouse are similar to those described by Payne (1966) for blackbirds (Agelaius), so will not be discussed here.

Postovulatory follicles were counted macroscopically in ovaries of laying and incubating hens captured 3 May through 21 June. The smallest ovary containing postovulatory follicles which could be counted macroscopically weighed 0.32 g. All ovaries from brood and lone hens required microscopic examination.

The ability to distinguish postovulatory follicles from atretic follicles decreases throughout the reproductive cycle. All laying and incubating hens had easily recognizable postovulatory follicles. Only 38% of yearling and 48% of adult brood hens and 50% of lone hens had postovulatory follicles that could be discriminated (Table 4), although all ovaries showed signs of some type of

regressing follicles. Only one ovary of the ten collected from hunter kills contained recognizable postovulatory follicles. This hen (an adult) had 2 size classes of postovulatory follicles, indicating that she had renested (Table 4). Most ovaries from hens killed by hunters contained postovulatory follicles or atretic follicles persisting as vacuolated or hyalinated areas, but they could not be differentiated. As the ovary decreased in size, so did the reliability of distinguishing postovulatory follicles. There was high individual variation in the length of time postovulatory follicles persisted in brood hens. For example, postovulatory follicles could be counted in some hens at least 43 days postovulation, but could not be distinguished in others at 27 days postovulation. Generally, in ovaries in which the age of postovulatory follicles could be determined, those older than 43 days could not be differentiated.

Adults always had more postovulatory follicles than yearlings (Table 4). Lone yearling hens had fewer than yearling brood hens, perhaps indicating that lone hens either deserted or had a partial clutch destroyed and did not renest. All incubating, brood, and lone hens had brood patches and all had ovaries which showed signs of regression of follicles, indicating that presence of brood patch is a reliable indicator of reproductive activity.

In ovaries in which the total number of ovulations could be counted, the mean number for yearlings was

6.23±0.30SE (N=13, range=4-8), less than the adult mean of 8.92±0.75SE (N=12, range=5-13) (Mann Whitney U test, $p<0.01$). One yearling (7%) and 5 adults (42%) had ovaries in which 2 size classes of regressing postovulatory follicles persisted, indicating that they had renested. Removing from the calculation birds which renested, the mean number of postovulatory follicles was 6.08±0.29SE (N=12, range=4-7) for yearlings and 7.14±0.46SE (N=7, range=5-8) for adults. These were significantly different ($p<0.05$).

Discussion

Although individual laying histories were not known, the number of postovulatory follicles appears to be indicative of the clutch size in blue grouse. Zwickel (1975) reported a mean clutch size for adults of 7.30±0.18SE (N=33), and 5.65±0.27SE (N=20) for yearlings. This compares closely to the number of postovulatory follicles found histologically in this study of 7.14±0.46SE (N=7) for adults and 6.08±0.29SE (N=12) for yearlings, indicating that dump nesting is likely not a common occurrence in blue grouse, as it is in ring-necked pheasants (Phasianus colchicus) (Meyer et al. 1947) and chukar (Alectoris graeca) (Mackie and Buechner 1963).

The length of time over which postovulatory follicles can be counted in ovaries of different species varies considerably: 6 months postovulation for ring-necked pheasants (Kabat et al. 1948); 10 days postovulation in California quail (Lophortyx californicus) (Lewin 1963); and through August of the same breeding season in blue grouse (Standing 1960). Payne (1966) suggested that counting pigmented remains macroscopically could lead to errors, since regressing atretic follicles could be counted as well.

This study indicates that postovulatory follicles can be distinguished macroscopically from atretic follicles

throughout laying and part of incubation. However, histological procedures must be used for ovaries of brood and lone hens. One can identify postovulatory follicles histologically up to approximately 43 days postovulation, though this varies considerably with individual hens. The technique does not appear valid for assessing egg production of hens shot during hunting season in August. Although the ovaries contain vestiges of regressing follicles, it is impossible to distinguish postovulatory follicles from regressing atretic follicles in most cases.

The gonadal cycle of female blue grouse resembles that described for the chukar (Mackie and Buechner 1963), California quail (Lewin 1963, Williams 1967) and other periodic breeders. The cycle consists of a two-phased period of recrudescence: a slow phase followed by rapid development. After laying, a period of rapid regression is followed by a slower phase. The pattern is similar to that reported by Standing (1960) for female blue grouse in Washington, except that birds in the Washington population laid earlier. Follicles of hens in this study developed to ovulation size in the fast recrudescence phase over a period of 9-10 days.

Yearlings begin the breeding season with smaller follicles and oviducts, lay later at a lighter oviduct weight and regress sooner to a lower oviduct weight than adults. Lighter oviducts in yearlings persist at least until the end of August. The ovary is also lighter in

yearlings in August, but follicles attain adult size during laying, indicating that yearlings and adults likely lay eggs of equal size, even though the clutch size of yearlings is smaller (Zwickel 1975). Yearling ring-necked pheasants lay fewer eggs but of similar weight to adults (Labisky and Jackson 1969).

Yearling blue grouse hens are thought to be less capable of renesting than adults (Zwickel and Lance 1965). The ovary of one yearling in this study revealed two size classes of postovulatory follicles indicating that she had renested. Forty-two percent of adults in which postovulatory follicles could be counted had renested. Zwickel and Carveth (1978) reported that 37% of 164 nests of blue grouse did not hatch. Thus, most adults are capable of renesting if the first clutch is destroyed or deserted, while this appears to be rare for yearlings, another indication of their lower reproductive potential. The higher incidence of renesting in adults likely accounts for their longer duration of laying. There was no indication of a hen renesting more than once.

The lower gonadal weight of yearlings and reduced capability of renesting suggests that lower clutch size in yearlings is due to physiological immaturity. In many species, birds breeding for the first time have a smaller clutch size (for review see Lack 1966). Lack attributed lower clutch size to inexperience in finding food. Zwickel (1975) argued that if inexperience in finding food caused

lower clutch size, it might also affect hatchability and fertility, which are similar in adult and yearling blue grouse. He concluded that smaller clutch size, at least in blue grouse, is most likely related to physiological maturity. Labisky and Jackson (1969) support this view. They reported that captive ring-necked pheasants maintained on the same diet, laid more eggs as adults than as yearlings.

Delay in yearling breeding cycles has not received as much attention in the literature as the contoversy about clutch size. In some species (e. g. California quail (Lewin 1963)), yearlings have smaller ovaries than adults early in the breeding season, but the ovaries achieve adult size and the birds begin to lay at the same time. Leinonen (1973) noted that although first year white wagtails (Motacilla alba) arrived on the breeding range later than adults , they laid at the same time. In species in which yearlings do lay later, there has been some suggestion that social interaction with adults may cause the delay. Crawford (1977) reported that yearling red-winged and yellow headed blackbirds (Agelaius phoeniceus and Xanthocephalus xanthocephalus respectively) nested later and had smaller clutches than adults. Yearlings migrated later than adults and adult females actively defended their territories against other females. Crawford suggested that this social interaction with adults may cause yearlings to breed later. Inhibition of reproductive activity was reported by

Christian (1971) in several species of rodents living in populations at high density with high levels of agonistic behavior.

Zwickel (1977) noted that most yearling blue grouse do not breed until adults are on nests and suggested that adults may suppress yearling breeding activity. My results support this view, indicating that yearlings, although usually lagging behind adults in reproductive events by one week are capable of laying earlier when adult numbers are low. Possibly the slow stage of recrudescence can be lengthened or shortened depending on how soon a yearling can find a place in the breeding population. Adult hens may actively interact with yearling hens, inhibiting yearling gonadal development.

Acknowledgements

This study was carried out with the assistance of F. C. Zwickel who, as well as being a thought provoking colleague, provided free access to his data and other material, field support and critical comment on the paper. R. A. Lewis, J. O. Murie, J. Roland and L. Sopuck gave useful criticism of the manuscript. C. Kulman and C. Westoll provided summer assistance. J. F. Bendell lent me specimens and assisted with the histology. The study was supported by the National Research Council of Canada, The British Columbia Fish and Wildlife Branch and the University of Alberta. Work was conducted on lands of Crown Zellerbach of Canada, Ltd., Courtenay Division.

Table 1. Mean weights of ovaries and oviducts of hens killed by hunters, Aug. 28,29 1976.

Adults	Yearlings	Juveniles
	Mean ovary weight (g)	
0.25±0.025SE	0.16±0.007SE	0.05±0.003SE
(n=12)	(n=9)	(n=8)
	Mean oviduct weight (g)	
0.53±0.03SE	0.35±0.03SE	----------
(n=10)	(n=7)	

Table 2. Laying periods, oviduct weights, and diameters of largest preovulatory follicles in laying adult and yearling hens.

	Adults	Yearlings
Laying period	May 2-June 16 (n=12)	May 10-June 7 (n=28)
Oviduct weight ($\bar{X}$+SE)	25.49±0.99SE (n=12)	21.57±0.51SE (n=28)
Diameter largest preov. follicle ($\bar{X}$+SE)	28.87±0.71SE (n=10)	29.66±0.60SE (n=26)

Table 3. Mean dates of laying first egg for adult and yearling females at Upper Tsolum Main, 1976, and at Tsolum Main, 1974, 1975 and 1976.

Adults	Upper Tsolum Main 1976	13 May	(n=10)
Yearlings	Tsolum Main 1976	16 May	(n=8)
Yearlings	Upper Tsolum Main 1976	24 May	(n=6)
Yearlings	Tsolum Main 1975	24 May	(n=9)
Yearlings	Tsolum Main 1974	26 May	(n=6)

Table 4. Parameters associated with the post-breeding reproductive cycle of hens, 1970 and 1976, (POFs=Postovulatory follicles).

	Yearlings			Adults			Adults and Yearlings	
	Laying	Incubating	Brood	Laying	Incubating	Brood	Lone	Hunter kills
Dates collected	May 14-June 3	June 3-June 21	June 23-July 23	May 10-June 16	May 25-May 31	June 17-July 21	June 23-July 12	Aug. 28, 29
N	17	4	24	13	2	21	10	10
Percent with brood patch	12	100	100	23	100	100	100	?
Percent in which POFs distinct	100	100	38	100	100	48	50	10
No. POFs								
$\bar{x}$	2.88	6.75	6.00	3.15	8.00	9.10	5.20	13
SE	0.44	0.25	0.41	0.56	0	0.90	0.37	0
N	17	4	9	13	2	10	5	1
Ovary weight (g)								
$\bar{x}$	23.67	1.38	0.22	25.60	6.75	0.31	0.33	0.22
SE	2.56	0.55	0.01	4.03	5.45	0.04	0.04	0.02
N	15	4	22	8	2	21	10	10

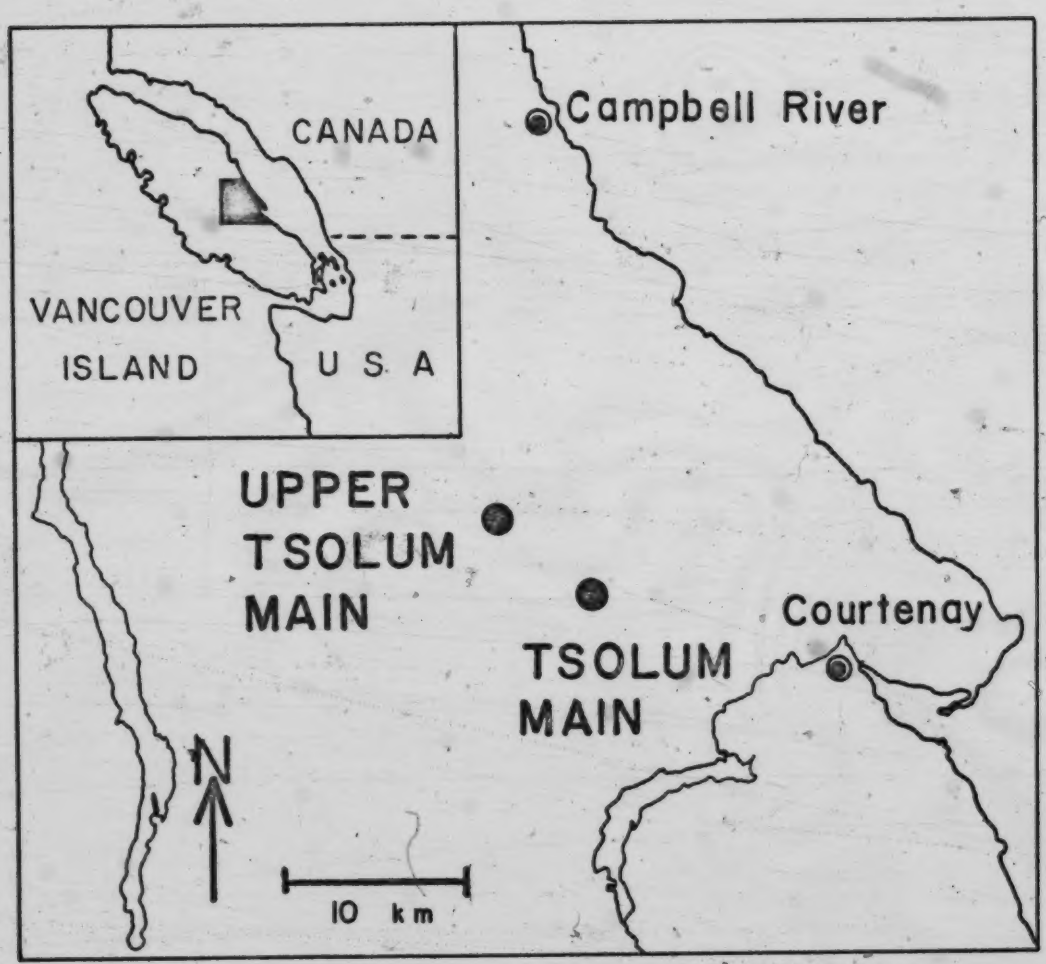

Figure 1. Study areas on Vancouver Island.

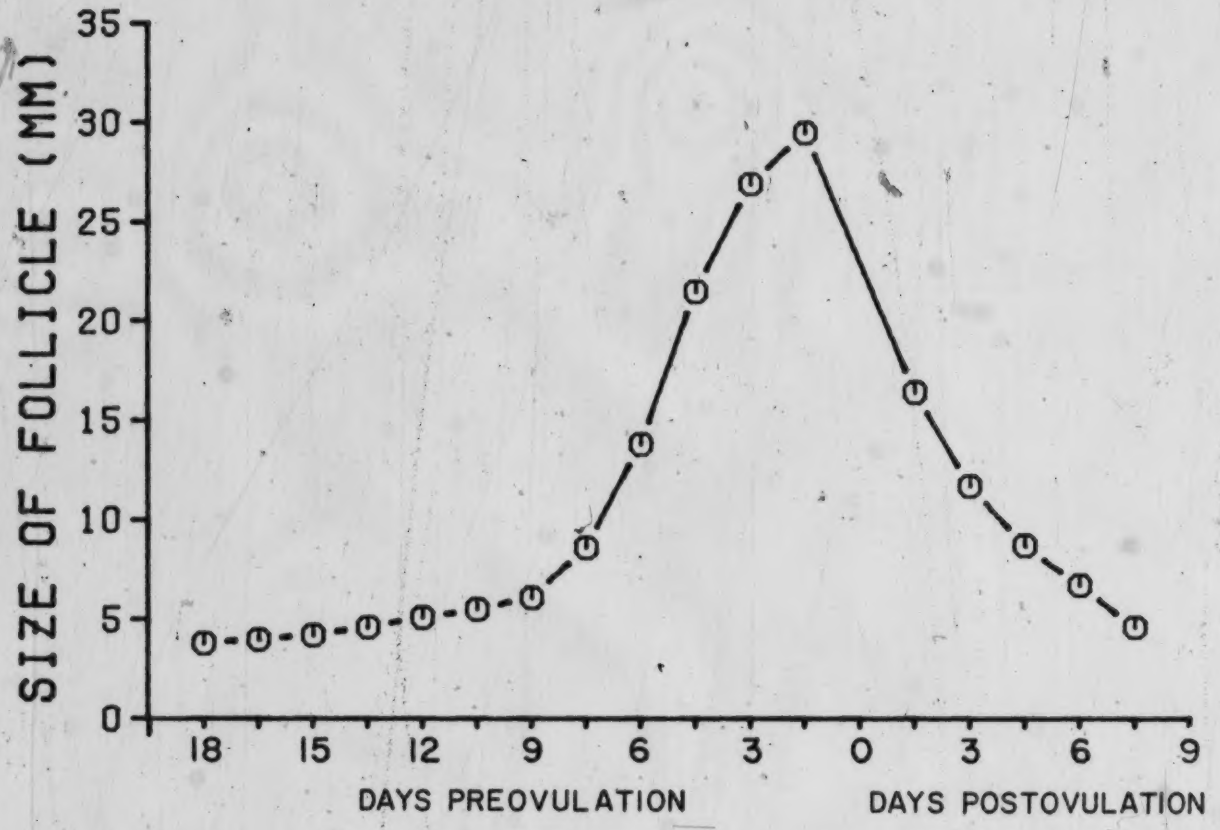

Figure 2. Preovulatory recrudescence and postovulatory regression of follicles (means of size classes).

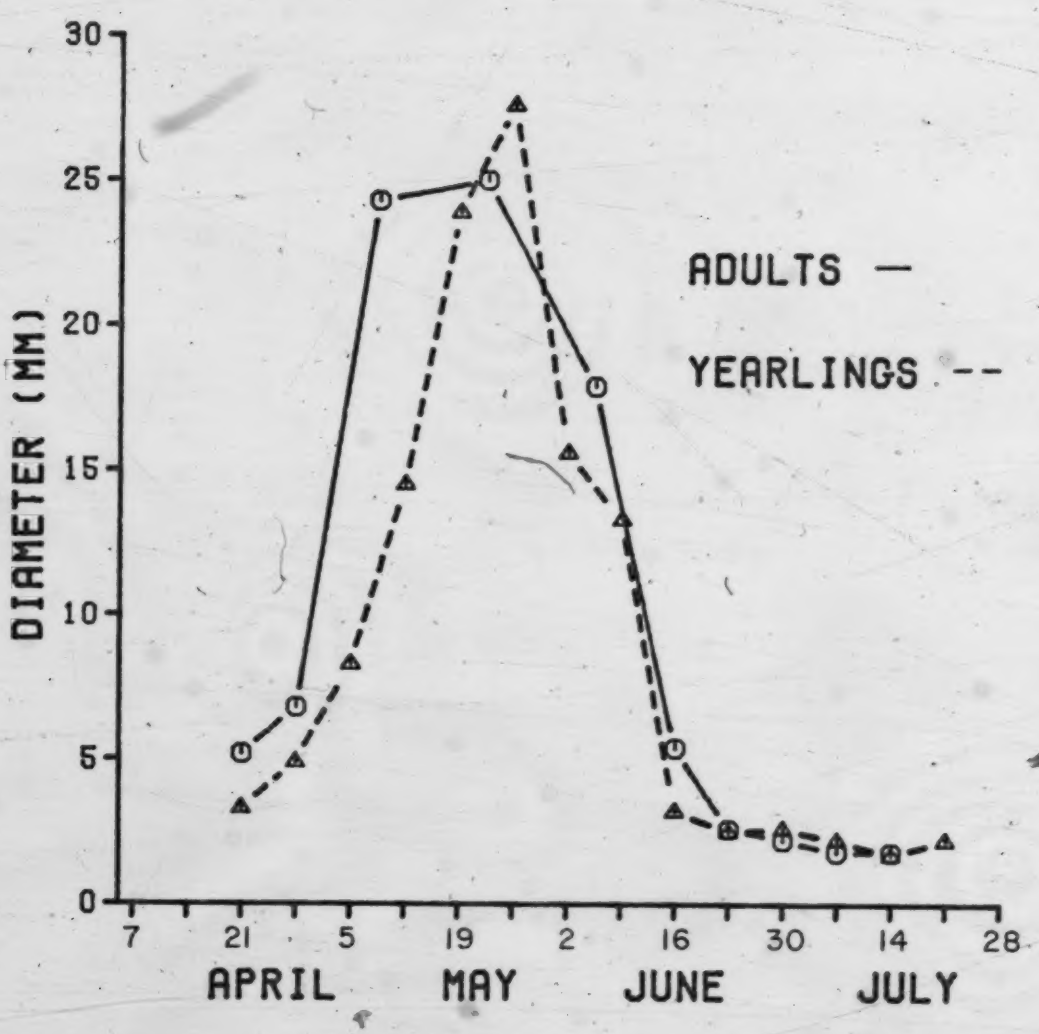

Figure 3. Seasonal variation in the mean weekly or biweekly diameters of largest unovulated follicles in adult (N=54) and yearling (N=145) females.

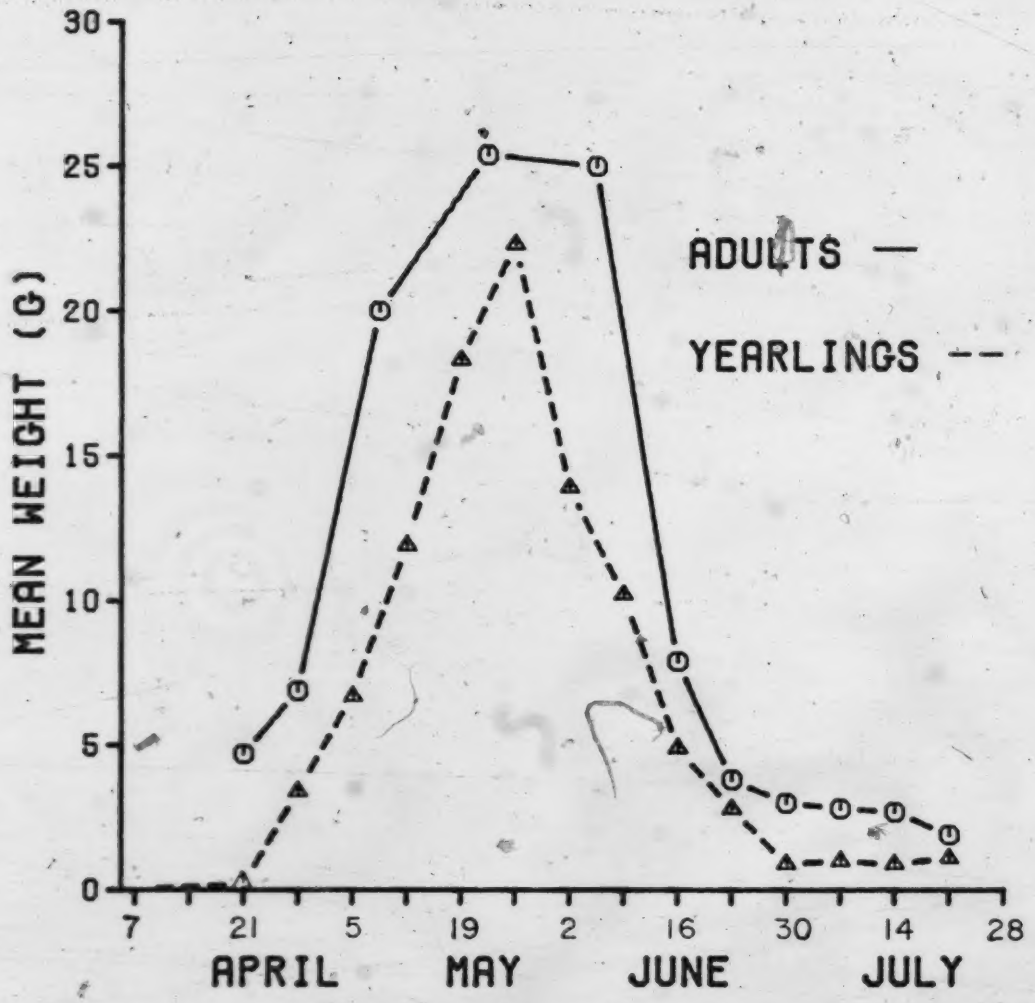

Figure 4. Seasonal variation in the mean weekly or biweekly weights of oviducts for adult (N=69) and yearling (N=198) females.

DATE	AREA	AGE	PEAK HATCH PERIOD	TOTAL NUMBER OF ADULTS
1971	TSOLUM MAIN	ADULT	7 5	30
		YEARLING	10 6	
1974	TSOLUM MAIN	ADULT	14 18	106
		YEARLING	4 3	
1975	TSOLUM MAIN	ADULT	7 20	118
		YEARLING	18 3	
1976	TSOLUM MAIN	ADULT	9 3	44
		YEARLING	3 6	
1976	UPPER TSOLUM MAIN	ADULT	6 4	—
		YEARLING	3 3	

18 25 2 9

JUNE JULY

WEEK BEGINNING

Figure 5. Periods of peak hatch for adult and yearling females in years of normal and low numbers of adults.

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PAPER 2. CHARACTERISTICS OF NON-BREEDING AND BREEDING FEMALE BLUE GROUSE

Abstract

Two groups of yearling females were identified from a series of blue grouse (Dendragapus obscurus fuliginosus) examined on Vancouver Island, British Columbia. Birds collected during a continuous yearling-only removal had a high proportion of non-breeders when compared to successful recruits. Early presence on the breeding range did not increase or decrease the chance of recruitment to the population, but heaviest birds were most likely to recruit.

Introduction

Parallel studies on increasing (Zwickel 1972) and decreasing (Bendell et al. 1972) populations of blue grouse on Vancouver Island demonstrated that large numbers of yearlings were available in spring for recruitment to areas which had been largely depleted of resident birds the previous year. Replacement of former residents was mainly by yearlings, indicating that yearlings, not adults, are the recruiting individuals in spring. These data suggest that a "surplus" of yearlings exists in spring and that these birds are excluded by residents. The fate of "surplus" birds is not known, nor are the factors determining which birds eventually enter the breeding population.

When only yearlings were removed from an experimental area on Vancouver Island, 1974 through 1976, more were collected than were identified on a nearby control area (Zwickel, unpublished data). This experiment again demonstrated the presence of "surplus" yearlings available for recruitment if others were removed. Thus, the collections from 1974 through 1976 should contain both "surplus" (non-breeding) and resident (potentially breeding) birds. If individuals in these two groups can be identified, comparisons can be made which could be important in determining factors which allow certain individuals to

enter the breeding population.

Using material collected from 1974 through 1976, I will demonstrate that two groups of yearling females did exist, and will compare these groups to answer the following questions:

1. Are non-breeding birds excluded before peak breeding begins, as suggested by Bendell et al. (1972) and Zwickel (1972)?
2. Do birds which are present on breeding areas early have a better chance of breeding than those arriving later?
3. Do non-breeding birds weigh less than breeders?

Study Areas

Specimens were collected from Tsolum Main and Upper Tsolum Main as described elsewhere (Hannon 1978). These areas are 2 to 3 km apart. Comox Burn, located 2 km south of Tsolum Main, was used as a control area. For a more complete description of study areas see Zwickel (1977) and Hannon (1978).

Methods

The following measurements from collected hens were used in this study: weight of oviduct, size of largest unovulated follicle, and total body weight.

Weight of oviduct was used as the main indicator of reproductive status for several reasons: Mackie and Buechner (1963) noted that weight of oviduct varied less than ovary weight during the breeding period because of the rapid change caused by follicular development and ovulation, several ovaries had lost yolk from follicles through mishandling or shot penetration, and oviducts are extremely sensitive to changes in estrogen level (Sturkie 1965).

Weights of oviducts up to 22 May (when most hens had started laying) are described by the following regression equations (appendix 1):

$$\text{ADULTS } Y=0.04 + 0.88X \quad (p<0.05)$$

$$\text{YEARLINGS } Y=-3.73 + 0.63X \quad (p<0.01),$$

where X=date and Y=oviduct weight.

Mean oviduct weight for laying hens is 25.5 g for adults and

21.6 g for yearlings (Hannon 1978). The time required for the oviduct of each pre-laying specimen to reach the size attained during laying was determined using the above equations. A hypothetical date for laying of the first egg for each collected hen was calculated by adding this time period to the capture date.

Date of laying of first egg was calculated for brood hens on Tsolum Main, Upper Tsolum Main, and Comox Burn 1974 through 1976 as follows: the mean age of brood was determined (Zwickel and Lance 1966, Redfield and Zwickel 1976) and added to 26 days (for incubation) plus 9 days (for laying) (Standing 1960), and the total subtracted from capture date. Data from Comox Burn were adjusted to conform to those at Tsolum Main and Upper Tsolum Main (Zwickel (1975). This correction brought the peak of laying into synchrony at all areas. These birds were used as a control against which collected birds could be compared. Peak laying was defined as the consecutive 2 week period in which most first eggs were laid.

Assuming the removal experiment allowed certain birds to be captured who would not have bred and whose gonads were poorly developed, specimens were placed into a group using the following criteria:

1. had a calculated first egg date on or after the last day of peak laying of brood hens.
2. largest follicle was less than 6 mm in diameter (ovary in the slow phase of recrudescence, Hannon 1978).

3. both largest follicle diameter and weight of oviduct were less than the mean for all individuals captured the same week (Hannon 1978).

All specimens fitting the first criterion, were then subjected to the second and third. Those that fit all three criteria were defined as non-breeders. The remainder were placed in a second group, termed breeders.

Results

Comparison of first egg dates between brood hens and collected birds.

Dates of laying first egg of collected adults (presumably resident birds) were determined for birds from Upper Tsolum Main, 1976. When these data were compared to values obtained by backdating from mean age of brood for individuals on Tsolum Main and Upper Tsolum Main 1976, the peak period of laying first eggs was the same for both groups (Fig. 1). This is the expected result if each group contained resident birds only. Thus, the method for calculating first egg dates from weight of oviduct appears acceptable.

Dates of laying of first egg were plotted for yearlings with brood on Comox Burn, Tsolum Main, and Upper Tsolum Main and for collected yearlings on Tsolum Main, and Upper Tsolum Main (Fig. 2). Yearlings with broods had a peak laying period from 21 May to 4 June, whereas collected birds had a peak laying period 28 May to 11 June, a week later. When the distribution of these 2 groups after the end of peak laying (4 June for brood females) was compared, 13% (13/97) of brood females and 44% (37/85) of collected birds would have laid first eggs after 4 June (X^2= 20.63,

$p<0.01$). Some collected birds would have laid significantly later than residents. Clearly, there was a large group of collected yearlings which, had they lived and bred, would have laid their first eggs later than most members of the population. Thus, there are 2 groups of yearlings present in the 1974-1976 collections, what I term non-breeders and breeders .

Comparison between collected non-breeding and breeding yearlings

Thirty-nine non-breeders and 46 breeders were identified among collected yearlings using the three criteria noted above. Differences between the 2 groups may help explain why certain yearlings are excluded from the breeding population.

Presence on breeding areas

Dates of removal give a relative comparison of presence of birds on the breeding range and are plotted for non-breeders and breeders in Fig. 3. Both classes of birds were captured in April. Arriving early does not appear to give an individual an advantage for recruiting. Zwickel (1972) suggested that exclusion of yearlings had finished by peak breeding (7 May on Tsolum Main, (Zwickel 1977)): 35% of

non-breeders were captured after that date, indicating that non-breeding yearlings were still present on the area after peak breeding began. However, only 3% of non-breeders were captured after peak laying for yearling brood hens had begun (21 May (Zwickel 1977)). Twenty-two percent of breeders were captured after this date. Thus, recruitment of yearlings appears to stop after most yearlings have started laying, at least in populations in which a removal is taking place.

Although some non-breeders were caught early, they were captured over a shorter time period than breeders (Fig. 3 (Kruskal-Wallis test, $p<0.01$)) and were either not present or were not captured on the study area after most recruited yearlings began to lay eggs.

Body Weight

Mean body weights of non-breeding and breeding females were compared with an unpaired t-test (Table 1). Only body weights of hens captured before 17 May were used since few non-breeders were captured after that date. Breeding females weighed more than non-breeders both when total body weight was compared and when body weight minus the gonad was compared ($p<0.01$). Breeders may recruit because they weigh more or they may weigh more because they have recruited and are building up resources for egg laying and incubation (Redfield 1973). Therefore, birds captured early

in the season (before 4 May), before body weight increases are significant, were compared (Table 1). Birds classified as breeders weighed significantly more than non-breeders ($p<0.05$).

Discussion

My results indicate that the process of exclusion of non-breeding or "surplus" yearlings is not a sudden phenomena occurring before peak breeding as suggested by Bendell et al. (1972) and Zwickel (1972). Rather, it appears that a group of wandering yearlings exists on the breeding areas until late May and when space is made available by mortality or other factors some of these yearlings may settle and breed. Others seem to disappear during peak laying.

Hens without a brood patch are rarely caught on the study areas in late June, July, or August (Zwickel and Bendell 1967), indicating that most hens found in late summer have laid eggs, and hence had successfully recruited. Perhaps non-breeding females migrate to winter range earlier than other birds, as do non-breeding yearling males (Bendell and Elliott 1967). Or non-breeding hens may travel widely or remain in suboptimal habitat where they would be less likely to be captured. The fate of non-breeding yearlings has yet to be discovered.

What factors allow some yearlings to recruit while others do not breed? Early presence on the breeding range does not appear to confer special advantage, but hens which weighed more seemed more likely to breed. Perhaps larger

birds are more capable of securing a home range or nest site and protecting it against intruders. Certainly other possibilities remain to be tested such as aggressiveness and general body condition of potential recruits. The problem remains of identifying who breeding and non-breeding birds are, particularly when studying live birds.

Acknowledgements

I thank J. O. Murie, J. Roland, and F. C. Zwickel for critical comment on the manuscript. F. C. Zwickel allowed free access to material and data collected over a number of years. This study was supported by the National Research Council of Canada, the University of Alberta, and the British Columbia Fish and Wildlife Branch. Studies were conducted on lands of Crown Zellerbach Canada, Ltd., Courtenay Division.

Table 1. Mean body weight of non-breeding and potentially breeding yearlings.

	Non-breeders	SE	N	Breeders	SE	N
Total body weight	828.51	11.81	37	918.34	12.46	29
Body weight (no gonads)	825.24	11.69	37	902.97	11.37	29
Body weight April to 4 May	803.00	23.08	14	912.50	22.51	8

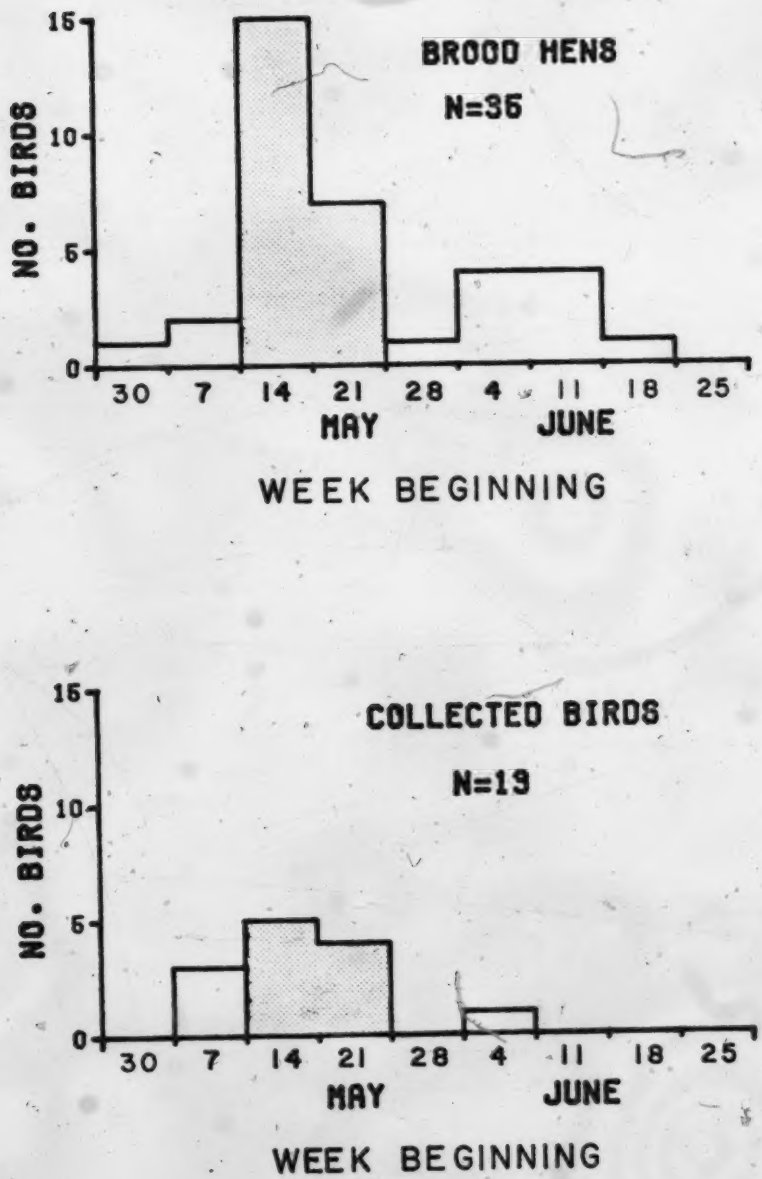
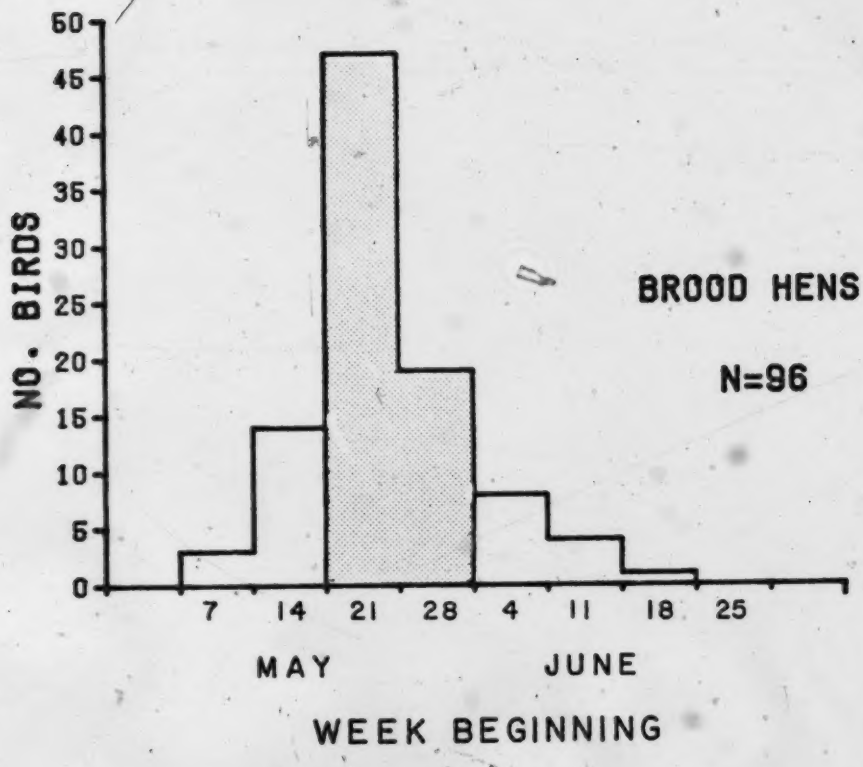


Figure 1. Extrapolations of first egg dates for adult brood hens and collected adults. Peak periods of laying are shaded.



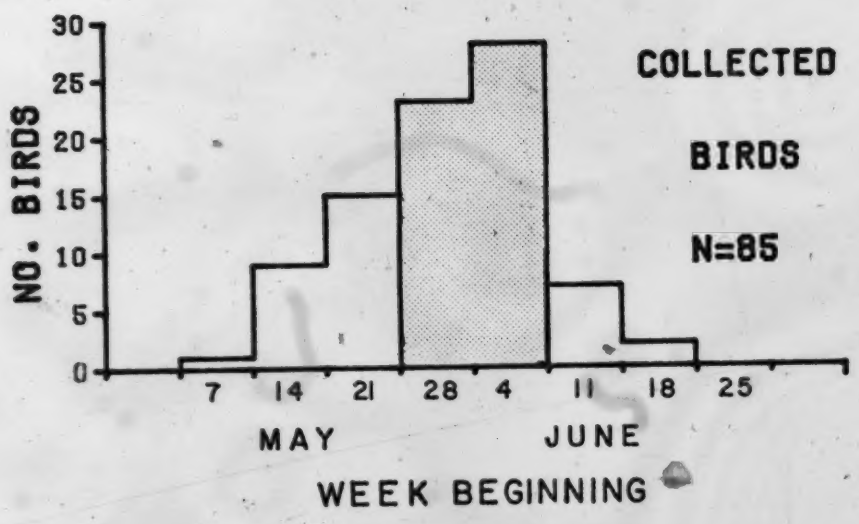


Figure 2. Extrapolations of first egg dates for yearling brood hens and collected yearling females. Peak periods of laying are shaded.

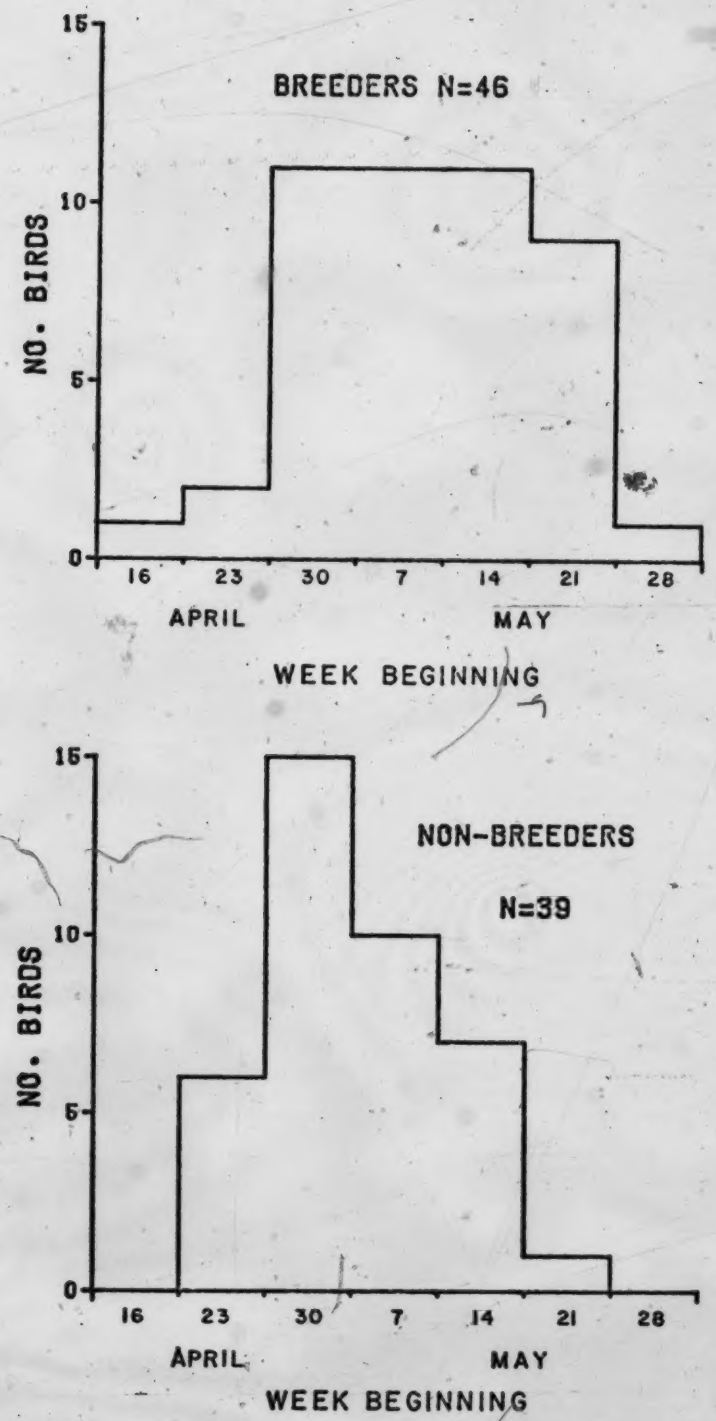


Figure 3. Date of removal (weekly groups) of breeding and non-breeding collected yearling hens.

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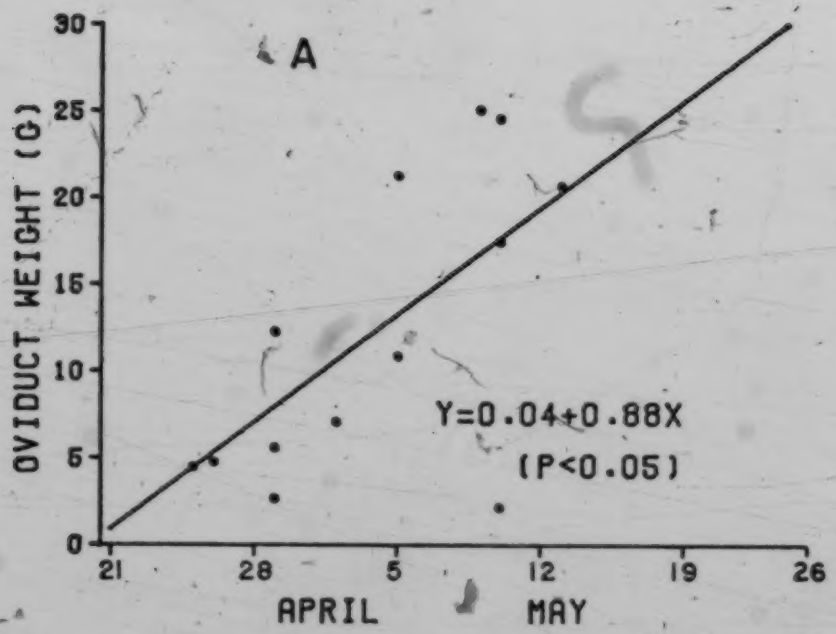
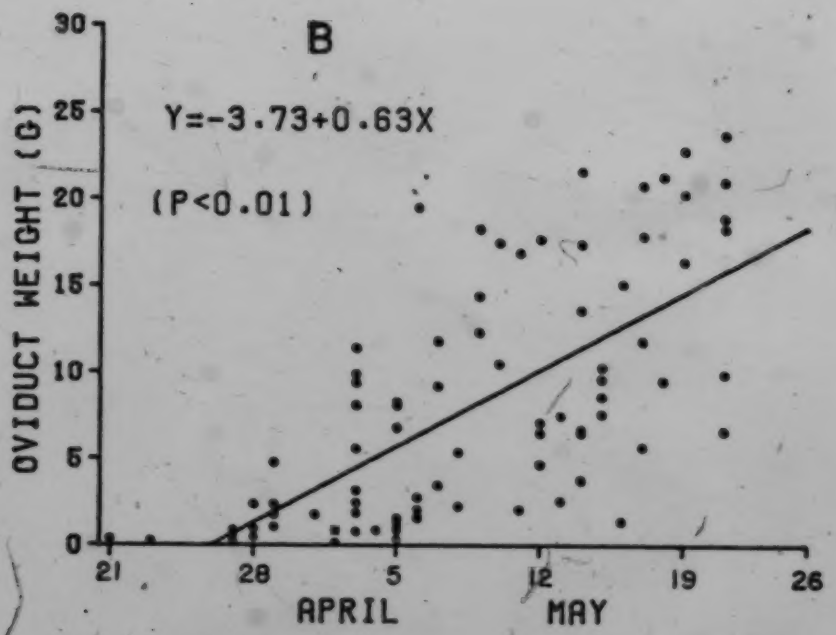
Appendix 1: Regression lines of oviduct weight against time





Appendix 1. Weights of oviducts up to 22 May (when most hens have started laying) with Bartlett's regression lines for adult (A) and yearling (B) females.

PAPER 3. PLASMA CALCIUM AS AN INDICATOR OF REPRODUCTIVE CONDITION IN FEMALE BLUE GROUSE

Abstract

Measurement of total plasma calcium as an indicator of reproductive status of live blue grouse (*Dendragapus obscurus fuliginosus*) hens was assessed. Total calcium showed a high positive correlation to weight of oviduct and development of ovarian follicles. Hens with ovaries in the slow recrudescence phase could be readily distinguished from laying hens or those with ovaries in the rapid stage of recrudescence. The method was not sensitive enough to predict the precise time of ovulation.

Introduction

This study was initiated to develop a method for assessing the reproductive condition of live female blue grouse in the wild. Direct measurement of estrogens, perhaps the best indicator of reproductive status, is costly, time consuming and requires larger amounts of plasma than are usually available from field studies. Estrogens, however, cause increased levels of other constituents of the blood, such as calcium, phosphorous, and lipids (Sturkie 1965). These materials can give an indirect measure of estrogenic activity. Calcium, in particular, can be quantified easily and inexpensively in relatively small volumes of plasma and shows a 2 to 3-fold increase in concentration in the plasma of ovulating chickens and pigeons (Sturkie 1965, Simkiss 1967).

The objective of this study was to ascertain whether total calcium in the plasma of wild female blue grouse on Vancouver Island, British Columbia, is a reliable indicator of the reproductive condition of the bird. Prior to this study, presence of a brood patch indicated that a hen was incubating (Zwickel and Bendell 1967) but laying and pre-laying hens could not be distinguished with certainty.

Methods

Calcium was measured in the plasma of 137 hens and 37 males (used as controls) collected in 1975 and 1976 and in a group of 40 live hens which were radio-tagged and monitored in 1976 and 1977.

Blood was removed either from the brachial vein (live birds) or by cardiac puncture (dead birds). Approximately one ml of blood was collected in a syringe which had been rinsed in 4% sodium citrate. Blood was placed in citrate-rinsed two ml capped vials and stored on ice until it was spun on a battery operated centrifuge, usually within 8 hours of collection. The plasma was then transferred to 0.5 ml vials and stored frozen.

Plasma was thawed in the laboratory and 50 ul were diluted with 5 ml of 1% KCl. Diluted samples were analysed for total calcium on a Jarrell-Ash Atomsorb Atomic Absorption Flame Emission Spectrophotometer. A standard curve was constructed by plotting concentrations in ppm against emission for prepared calcium standards of 1.0, 2.5 and 5.0 ppm. One sample from a homogenous pool of chicken plasma was analysed during each assay to standardize the procedure.

Ovary and oviduct were excised from all collected hens and weighed to the closest 0.01 g. The diameter of the

largest follicle of each ovary was measured with dial calipers to 0.01 mm.

Total plasma calcium was tested for correlation with weight of oviduct and size of largest follicle.

Accuracy of calcium as a measure of the reproductive condition of live birds was tested. Radio-tagged birds were placed in reproductive categories at time of capture based on the date they subsequently laid their first egg. This category was compared to their reproductive status as determined by plasma calcium level at time of capture.

Results and Discussion

Total calcium concentration related to weight of oviduct and follicular diameter in collected birds.

Both diameters of largest follicles and weights of oviducts showed high positive correlation with total plasma calcium ($R=0.758$ and 0.846, respectively, ($p<0.01$)). Calcium concentration is plotted against weight of oviduct up to laying in Fig. 1.

Follicles less than 6 mm in diameter in ovaries of blue grouse develop at a slow rate. When follicles reach 6 mm, the growth rate increases markedly, taking 9 or 10 days to reach ovulation size (Hannon 1978). Hens with follicles less than 6 mm in diameter had low calcium levels not significantly different from post-laying hens or males (Fig. 2). Level of calcium rose quickly as follicles enlarged, reaching a maximum level one to four days prior to ovulation of 2.7 times that of birds with follicles less than 6 mm in diameter. During laying, calcium concentration decreased slightly, likely due to diffusible calcium being removed for calcification of egg shells (Taylor and Hertelendy 1961).

Data were also analyzed in relation to 3 general stages in the ovarian cycle (Table 1): A, hens with follicles less than 6 mm wide (slow recrudescence, Hannon 1978); B, hens

with follicles greater than or equal to 6 mm, including ovulating hens; and C, post-laying hens. Post-laying hens could be distinguished from pre-laying hens by either the presence of a brood patch in live birds or postovulatory follicles. The mean calcium levels for birds in groups A and C were significantly different from that for birds in group B ($p<0.01$). Thus pre-laying hens in the slow phase of ovarian recrudescence can be separated from those which are in the rapid phase or are ovulating.

An assessment of the accuracy of reproductive categories based on calcium levels , using radio-tagged hens.

The reliability of recognizing group A or B birds based on their calcium levels was tested using a group of radio-tagged hens for which date of laying first egg was known (Hannon 1978).

Reproductive states of birds at time of capture were determined as follows: since rapid recrudescence of follicles occurs over a 9 day period (Hannon 1978), any bird with a difference of 9 or less days between capture and laying of first egg was considered in group B. All birds with a difference of greater than 9 days were considered in group A.

Birds were then assigned to groups based on their calcium levels. Since the maximum concentration for birds

in Group A was 160 ppm (Table 1), and this was also the upper range for males, any bird with a calcium concentration greater than 160 ppm was placed in group B, and those with calcium less than or equal to 160 ppm were placed in group A. These data are summarized in Table 2. When birds grouped by calcium level were compared to those by date of laying first egg, over 90% of the birds (37/40) were assigned correctly using the calcium concentration method. Three birds were assigned to group B based on calcium concentration when they were actually in group A.

To assess how accurately plasma calcium concentration reflected the precise reproductive state of birds, oviduct weights were extrapolated from the regression line in Fig. 1, using calcium concentration at capture. Oviduct weights were then used to extrapolate the number of days required to attain egg-laying size . Since date of laying of first eggs was known for radio-tagged hens, the actual and calculated dates could be compared. Only fifty-six percent of the birds were assigned a date of first egg within a week of the actual date. Thus, calcium concentration appears too variable to reliably assess precise reproductive condition of hens.

In summary, precise reproductive status of a bird cannot be determined using calcium concentration. However the method does allow one, with over 90% certainty, to decide whether a live bird is in the slow phase of ovarian recrudescence or the rapid phase of recrudescence and

ovulation. Beyond this, active breeders can be identified by the presence or absence of a brood patch, thus allowing three categories of breeding status to be identified.

Acknowledgements

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Table 1. Mean total calcium (ppm) in the plasma of hens in three reproductive categories: A, slow recrudescence; B, fast recrudescence or ovulation; C, post-laying.

	Reproductive Category		
	A	B	C
	follicles <6mm	follicles >6mm	post-laying
$\bar{x}$	118	260	110
Range	70-160	75-470*	55-200
SE	3.4	9.0	4.5
N	31	64	41

* all but 3 samples exceeded 160 ppm.

Table 2. Comparison between reproductive group based on date of laying of first egg and reproductive group based on calcium concentration.

Group	Number	Calculated number
A	31	28
B	9	12
%correctly assigned	93%	

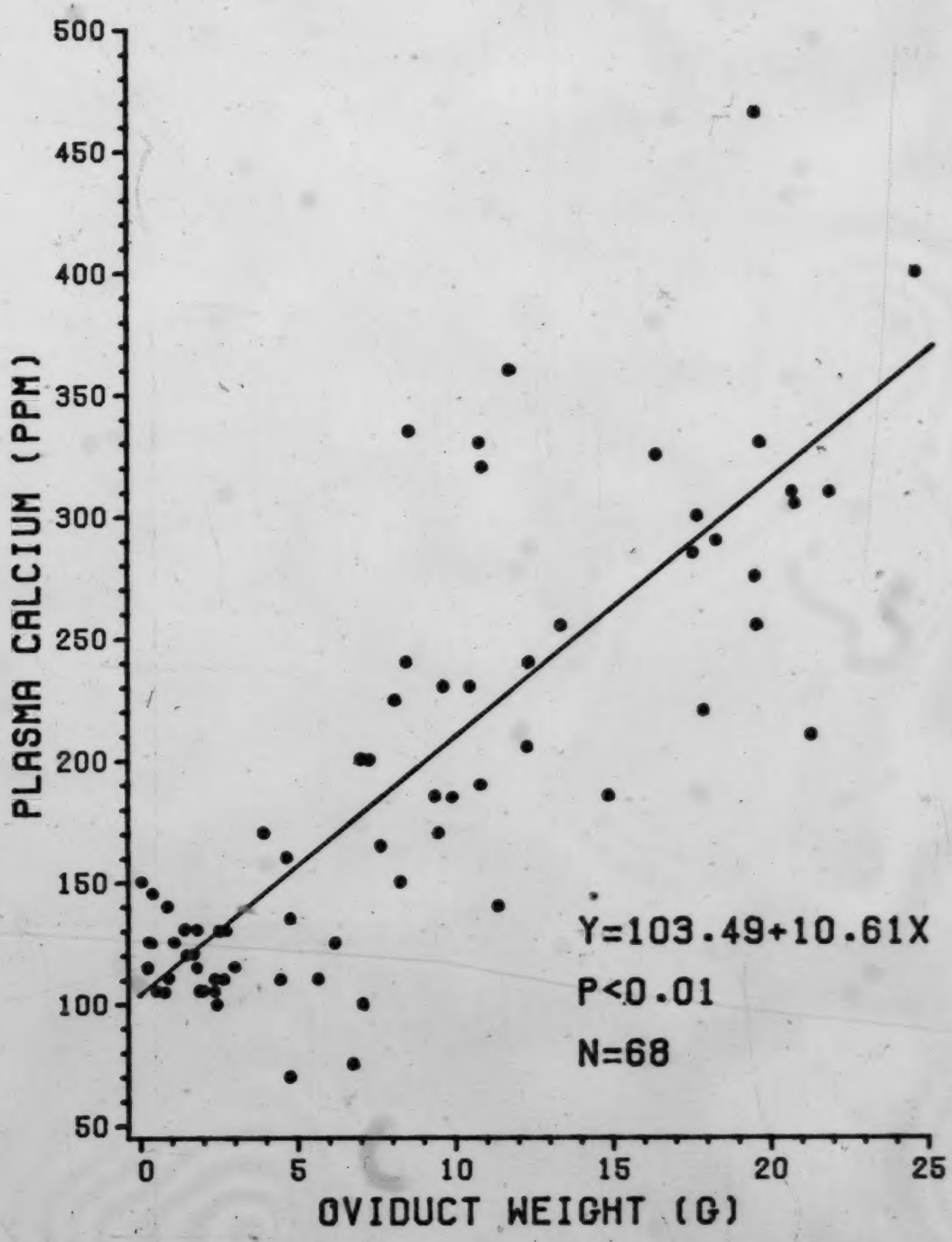

Figure 1. Plasma calcium concentration plotted against weight of oviduct.

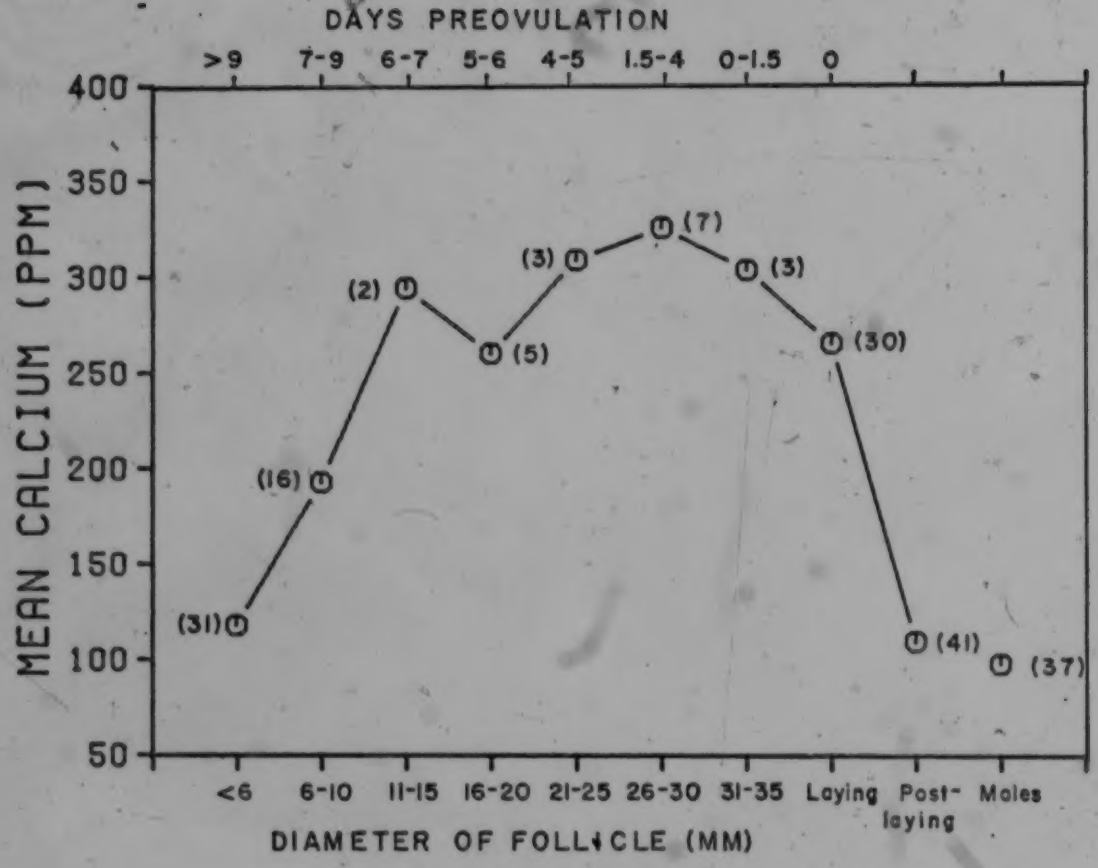

Figure 2. Mean plasma calcium in pre-laying hens with increasing follicle diameter, laying and post-laying hens, and males (sample size in brackets, days preovulation from Hannon (1978)).

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PAPER 4. MOVEMENTS AND BEHAVIOR OF FEMALE BLUE GROUSE DURING THE PRE-NESTING PERIOD

Abstract

Movement patterns and other behavior were compared for adult and yearling female blue grouse (Dendragapus obscurus fuliginosus) during the pre-nesting period. Yearlings moved over longer distances than adults and localized later in the reproductive season, just prior to rapid recrudescence of the gonads. Hens responded to a taped aggressive call (the cackle) over a short period of time in spring. Highest incidence of cackling was related to peak copulation and laying of first eggs. Yearlings cackled later than adults. Hens may space themselves on the breeding range by mutual avoidance, using the cackle to advertise their presence on a localized area to other hens.

Introduction

Territoriality and social behavior of male tetraonids has received much attention in the literature. There is, however, a distinct paucity of information on these subjects for female grouse. Spacing of hens and the behavior which causes it may be of particular importance in regulating numbers of animals, especially in polygynous or promiscuous species.

The blue grouse is a promiscuous species with an equal sex ratio (Zwickel and Bendell 1967a). Yearling and adult hens may breed but only adult males are likely to copulate (Bendell and Elliott 1967). Speculation is increasing that adult hens may limit the number of yearling hens which breed (Zwickel 1972, Zwickel 1977). Studies in which sizeable portions of the breeding population were removed indicate that large numbers of yearlings of both sexes are available for replacement (Zwickel 1972, Bendell et al. 1972). The size of the breeding population was postulated to be regulated by the exclusion of some yearlings in early spring by resident adults. If so, adults must have some advantage over yearlings.

Differences between breeding adult and yearling females have been reported. Yearlings have smaller clutch sizes, (Zwickel 1975) and usually nest a week later than adults

(Zwickel 1977). Oviducts of adult hens develop sooner in the spring than those of yearlings (Hannon 1978). Zwickel (1977) reported that many yearlings do not breed until adults are nesting. He suggested that adults may suppress yearlings, who do not breed until they are established on the summer range. Recent evidence supports this view (Hannon 1978). Oviducts of yearlings developed sooner in years when adult numbers were low, than in years with more adults, enabling yearlings to nest at the same time as adults.

If adults supress yearling breeding activity and perhaps entirely exclude others, how is this achieved? Agression among females has rarely been observed in the field. The greatest reactions of captive blue grouse hens to their mirror images occurred during the breeding and egg laying period (Stirling 1965,1968). A call, termed the quaver cry (Stirling and Bendell 1970) or cackle accompanied aggressive encounters between caged hens. The call has been postulated to have either a reproductive or an aggressive function (Stirling 1965, Stirling and Bendell 1970) and may be important in interactions among hens in the wild.

The main objective of this study was to determine if there were differences between the movement patterns of adult and yearling hens in the pre-nesting period and to study their reactions to taped cackle calls. Behavior of hens will be discussed in relation to their reproductive status. Implications of the cackle in interactions among

birds will be considered.

Study Areas

This study was conducted on the east slope of Vancouver Island 16 km west of Courtenay, British Columbia, in the spring and summers of 1976 and 1977. Three principle study ares were used: Comox Burn, a 485 ha densely treed area; Tsolum Main a 625 ha more open area, 2 to 3 km northwest of Comox Burn; and a 600 ha buffer area between the two. The buffer area was more similar to Tsolum Main than to Comox Burn in terms of vegetative succession. The areas were logged, burned and replanted with Douglas fir (Pseudotsuga menziesii) at varying times between 1961 and 1969. For more detail see Zwickel (1972,1977).

Methods

Movements of radio-tagged hens

During April 1977, four yearling and five adult hens were captured using a telescoping noose pole (Zwickel and Bendell 1967b). A sample of blood was removed from the brachial vein of each hen for analysis of plasma calcium concentration (Hannon 1978). Birds were individually marked with colored leg bands and each fitted with a radio transmitter of the type used by Herzog (1977). The entire radio package weighed about 17 g, approximately 2% of the bird's body weight.

Each bird's movements were monitored until incubation had begun. Hens were usually located at least every second day. Each bird was either sighted or triangulated to within 5 m of its position using a hand-held yagi antenna. Triangulation was used to avoid flushing a flighty bird, or one hiding in very dense vegetation. At each location notes were taken on weather, habitat and behavior. The presence of other birds was recorded. Birds were later rated on a scale from 1-5 (1 being very tame, 5, very flighty) based on their behavior during observations over the entire study period. Locations were plotted on a gridded map .

The boundaries of the home range occupied by each

grouse were calculated using Harvey and Barbour's (1965) method, as modified by Herzog (1977). The size of the home range was determined using a computer program which calculated the area of the resulting polygon. The area of home range was calculated for three time periods: from capture to laying of first egg, to give a total area; from 15 April to laying of first egg, to give areas for comparison starting at the same point in time; and for 20 days before the first egg was laid, to compare birds over the same reproductive period since all birds had been captured at least 20 days prior to laying.

A bird was considered to be localized if, in any grouping of sightings related in time, it did not move away more than twice the distance of the two most widely separated points of that grouping.

Cackle transects

Four transects were established in the spring of 1977 to determine when females respond to the cackle and to assess how the cackle affects the vocalizations and behavior of other females and males. Transects, 2 on Comox Burn and 2 on Tsolum Main, were set up along logging roads. They were begun one hour before sunset, a period when grouse activity is high (Bendell and Elliott 1967). Each transect was run once a week, except from 6-17 April when only one

observer was available. Two transects were run concurrently, one at Comox Burn and one at Tsolum Main from 24 April to 2 June. A five minute tape of a series of cackles, each separated by 6 seconds of silence, was played at each of 5 stations at 400 m intervals. At each station, a female mounted in neutral posture (Bendell and Elliott 1967) was placed at the edge of the road and the observer hid nearby. For one minute, the total number of male songs (hooting), whoots (a single syllable call given during courtship of a hen), flutter flights (flight noise made by a territorial male) and female clucks, cackles, and whinnies were recorded (vocalizations and displays are described in Bendell and Elliott (1967) and Stirling and Bendell (1970)). The cackle tape was then played and all female responses (cackles, whinnies, or clucks) and the approach of any bird toward the female model were recorded. After completion of the tape, one minute was spent tabulating the same information noted during the pretape observation period. The observer then walked to the next station and repeated the procedure. To avoid possible bias, tape recorders, models, observers, and the direction in which each transect was done were alternated each week.

Cackle experiments

Individual experiments were conducted in spring of 1976 and 1977 to observe the reaction of hens to taped cackle calls and to determine the reproductive status of hens which cackled. Hens were located using a trained pointing dog or were found in the course of other work. Upon locating a bird, I retreated 15 to 20 m and hid behind vegetation for 15 to 20 minutes in silence. A taped cackle was then played during which time the female's vocalizations and behavior were noted. In 1976 the playback included 5 minutes of cackle proceeded by one minute of winter wren (Troglodytes troglodytes) song, the latter to determine if the tape noise was eliciting a response. Since no hen responded vocally to this call, in 1977 the tape consisted of one minute of silence followed by 5 minutes of individual cackles, each separated by 6 seconds of silence. In most cases, the hen could not be seen during the experiment and she could not see me. After the experiment, an attempt was made to capture the hen and/or read its leg bands. The location of the hen, presence of other birds and whether or not the hen approached, retreated, or remained stationary was noted. In 1976, 22 experiments were conducted from 13 April to 2 June, in 1977 18 experiments were undertaken between 23 April and 3 June.

In 1977 radio-tagged hens were also tested in the above fashion. Experiments were conducted with each hen at

varying times of day at least once every 5 days, if possible. A total of 68 experiments were performed between 9 April and 7 June.

Every effort was made to capture non-radio-tagged hens after experiments, to determine their ages and take blood samples for calcium analysis. However, this was not highly successful, perhaps due to the initial disturbance by myself or the dog. In order to increase the sample size from cackling hens, I played the tape along various roads on the study area, usually in the early morning or late evening on 10 days from 5 May to 23 May. If a hen responded an attempt was made to capture her.

Blood was taken from the brachial vein of all hens captured and analysed for total plasma calcium to determine the reproductive status of the bird (Hannon 1978). Birds with calcium levels less than 160 ppm were placed in reproductive category A, prelaying hens in the slow phase of ovarian follicle development, those with plasma calcium levels over 160 ppm were placed in reproductive category B, laying hens or pre-laying hens in the rapid phase of ovarian follicle development (Hannon 1978).

To compare the incidence of cackles to events in the breeding season, the ages of juveniles captured in 1976 and 1977 were determined by the method of Zwickel and Lance (1966) and modified as suggested by Redfield and Zwickel (1976). Date of hatch was determined by backdating. Dates of laying first egg and time of copulation were calculated

for each hen (Zwickel 1977).

Results

General information

All radio-tagged hens were captured between 4 and 15 April, 1977. Table 1 summarizes information collected at time of capture. Based on plasma calcium levels, all birds except #95 had ovarian follicles in the slow stage of ovarian recrudescence at capture. Female #95 had follicles in the rapid stage of development. Since it takes 9-10 days for follicles to develop to ovulation size during rapid recrudescence (Hannon 1978), and knowing the first egg date for each hen, all hens should have been in the slow stage of ovarian development.

Of the total sightings of radio-tagged hens in the pre-nesting period, only in 6.7% (12/179) of the cases were hens sighted with another hen close by.

Movements of pre-nesting hens

There appears to be a pattern in the movement of yearlings which distinguishes them from adults. Long distance movements between periods of localization are characteristic of yearlings (Fig. 1). All yearlings made a

sudden directicnal movement about 13 days prior to laying the first egg (Table 2), then localized, and eventually nested. Adults moved back and forth over much smaller areas (Fig. 2). Long directional movements in adults, if present, were made shortly after capture to an area of major use. For adults, the period of restriction of movement prior to laying is difficult to determine. If the definition for localization given in the methods is used, adults localized from 5 to 23 days before laying the first egg (Table 2). This large variability probably indicates that these figures are not meaningful measures for localization for adults as their general movements are much more restricted than those of yearlings throughout the pre-nesting period. The mean distance from initial capture site to eventual nest site is 4 times as long in yearlings as in adults (Table 3). Adults appear to arrive in April near to or on an area where they eventually nest, whereas yearlings move over a much greater area.

The area of home range occupied by pre-nesting hens was calculated for 3 time periods (Table 4). Mean home range was more extensive for yearlings than adults in all 3 periods. The exception was adult female #79 whose home range was comparable to that of female #64 and greater than female #55. Female #55 had a home range smaller than all adults in the period 20 days before she laid her first egg. Home range was smaller for birds 20 days pre-egg laying than after 15 April, indicating that the closer to egg laying,

the more localized movements become.

Cackle transects

On Comox Burn, the first cackling response was heard on 16 April and hens responded on most transects until 16 May (Fig, 3). On Tsolum Main, cackles were heard from 17 April to 12 May . Fourteen responses were heard at 81 stations on Comox Burn (17.3%) and 15 cackles were heard at 72 stations on Tsolum Main (20.8%).

On sixteen of 31 transects, mean hooting increased after the tape had been played. In 15 cases where hooting decreased or remained the same, there was a high incidence of whooting (66%). Whooting occurred most frequently when hens responded to the tape. Males respond to cackling females by approaching and giving the whoot, which then removes them from the hooting count. Whooting decreased markedly after hens ceased calling back to the tape (Fig. 3)

In 30% of the cases when hens responded to the tape, their cackles increased in volume, indicating that they were approaching the tape recorder.

Individual cackle experiments

Only 2 of the 9 radio-tagged females cackled in response to the tape. Perhaps they became habituated to the call. On 26 April, adult female #81 answered: she laid her first egg 17 May. On 16 May, yearling hen #65 cackled spontaneously and continued to call back to the tape when I played it. She laid her first egg 22 May.

In 1976, 6 non-radio-tagged hens responded to the tape by cackling. The first response was 20 April, the last 15 May. Two hens clucked, 10 remained stationary, 9 retreated and 2 approached the tape recorder. In 1977, responses occurred between 29 April and 20 May. Three hens cackled, one hen clucked, 12 remained stationary, 2 retreated, and in 3 cases movement was unknown. Data for 1976 and 1977 are summarized in Fig. 4. All adults responded before all yearlings.

Cackles were given in a period of one month's duration (20 April-20 May) and 35% of the hens tested during this time responded. Of hens that retreated, some may have done so during the 15 minute waiting period before the experiment began. Of hens that cackled back to the tape, none approached and one retreated from the speaker.

Non-experimental hens sometimes responded to the tape on occasions when I was unaware of their presence. During experiments with both radio-tagged and non-radio-tagged hens, there were 7 incidents of other hens cackling in

response to the tape between 21 April and 7 May. In 4 of 7 cases, hens approached the speaker and in one case the hen gave a whinny-like sound. These hens often placed themselves on prominent objects such as logs or trees while cackling.

When the tape was played along logging roads responses occurred between 5 and 10 May from 7 hens. These hens often approached the speaker or were located on a high log or stump. The tape was played until 23 May.

I observed 13 instances in which a male approached a cackling hen in courtship display or was heard whooting or hooting nearby. In 4 cases, hens ignored displaying males and continued calling in unison with another hen. One hen flew away and one ran away from a displaying male. Seven hens stopped cackling as soon as a male approached the area or was heard hooting nearby.

Occasionally cackling was heard without the stimulus from the tape. In 1976, six spontaneous calls were noted between 29 April and 17 May. Nine calls were heard in 1977 from 11 April to 16 May. Most spontaneous cackles were produced by single hens with no noted response from other hens. The majority were heard from 2000-2130 hours.

Reproductive status of cackling hens

Seven hens which cackled during 1976 and 1977 were subsequently captured. Calcium levels were measured in the plasma of 4 (3 samples were not useable) (Table 5). All 4 hens had high calcium levels which indicated that they were either laying or within 9-10 days of ovulation (Hannon 1978). Four hens (11158, 11236, and 11523) were fitted with radio transmitters at time of capture. Female 11158 apparently did not nest but ranged widely. Hen 11236 laid her first egg 8 days after capture. Female 11523 began to lay either the same day or the day after she had cackled, at a nest site close to where she was captured. Hen 11525 had a brood patch upon capture and hence was either incubating or possibly renesting.

Two females radio-tagged in April cackled later that spring (Table 5). Yearling hen #65 called 6 days before laying her first egg, close to her nest site. Adult hen #81 was heard cackling 21 days before she laid her first egg.

These results indicate that hens cackle at various times from 21 to 0 days prior to egg laying. Most of the yearlings called within 8 days of laying their eggs, adults were more variable. Six out of 8 hens cackled when they were in reproductive stage B (laying or pre-laying within 9-10 days of laying). Of the 2 others, both adults, one was in stage A and the other in stage C (post-laying).

Incidence of cackles compared to copulation and date of laying first egg.

Cackles heard in all contexts in 1976 and 1977 were grouped together by date. The period of peak hatch was one week earlier in 1977 than in 1976, hence to synchronize data, all cackles heard in 1977 were placed later in time by one week. Since Tsolum Main is usually one week behind Comox Burn in the period of peak hatch, data from here were placed earlier in time one week.

Incidence of cackles, timing of copulations and laying of first eggs are plotted in Fig. 5. The cackle tape was played at least 6 times per week from 9 April to 7 June in 1976 and 1977 combined. Cackles were heard 17 April to 23 May, with a peak 5 May to 11 May. This peak corresponds to peak copulation and the beginning of the first egg laying period. However, cackles were heard 10 days prior to the beginning of copulation, 14 days prior to laying of the first egg and ceased before all copulation was accomplished. Thus, most cackles were given when hens were in the rapid stage of ovarian development, and when many hens were probably localized on a home range. Hens which cackled in mid April were likely established adults.

Discussion

Few studies of movement patterns or other behavior have distinguished between adult and yearling birds. In species such as the blue grouse, in which yearlings are the recruiting individuals, differences between yearlings and adults could be important in identifying mechanisms of population regulation. Yearling movement patterns are strikingly different from those of adults. Adults move back and forth over a small area where they eventually nest and to which they show a high fidelity from year to year (Bendell and Elliott 1967, Boag 1966). Yearlings wander until they localize 11-15 days prior to laying eggs. The timing of localization was remarkably constant and compares favorably to the 12 days reported by Lance (1967) for 2 yearling hens also monitored by telemetry. This period is slightly longer than required for ovarian follicles to develop to ovulation in the fast phase of growth (Hannon 1978). Apparently follicles begin to enlarge rapidly only after the bird has settled near a nest site.

What causes this difference in movement patterns between adults and yearlings? Hannon (1978) postulated that adults inhibit yearling activity in some way. In populations with normal numbers of adults, yearlings lag behind them in reproductive events by a week. When numbers

are low, yearlings are not delayed (Hannon 1978).

Most yearlings arrive on the breeding ground already occupied by adults, and search for a nest site. They may settle briefly, but avoid adults if encountered, giving rise to long distance displacement. Some yearlings may find a vacant area because of adult mortality. When adults begin to incubate, they are removed for most of the day from interactions with other birds. Thus, other yearlings acquire access to part of the home ranges of adults and can settle. However, all yearlings do not find a place to nest. Perhaps interactions occur between wandering and established yearlings, or between wandering yearlings and renesting adults until it is too late for certain yearlings to breed.

If interactions among hens are indeed occurring, what form are they taking? I feel that hens probably do not engage in physical combat, but rather, maintain individual distance through aggressive vocalization. In no case in the pre-nesting period was a female model attacked by a hen even when the tape was played within 20 to 30 m of her.

The cackle has been postulated to have either a reproductive or aggressive role (Stirling 1965, Stirling and Bendell 1970, Cooper 1977). This call is primarly heard during the preincubation period, starting in mid-April when adult hens have returned to their home ranges. Their gonads may or may not have begun to develop rapidly, but they have not yet reached full breeding condition. Yearlings begin to cackle only when they are localized and within 9-10 days of

laying. Adults revealed more variability in reproductive status when they cackled, likely because they are settled over a longer period . Thus, cackles are heard over a limited time period, probably starting upon residency of a hen and ending prior to incubation. Herzog and Boag (1977) noted that female spruce grouse (Canachites canadensis franklinii) replied to an aggressive female call only when they were established on territories.

Since a vocalization is a form of communication, a hen must be imparting information to either males or females. A hen may cackle to attract a male. Males often respond to this call by whooting and approaching the female. However hens have been observed to flee from courting males or to ignore them to continue cackling in unison with another hen. Since some cackles are heard in early April, before most hens are in breeding condition, it appears that hens are not informing males that they are ready to mate. I do not agree with Stirling and Bendell's (1970) suggestion that this call synchronizes the breeding cycle of hens and cocks. According to Simard (1964), adult males are in breeding condition over a longer time period than females, and are capable of copulation in early April, before cackles are first heard.

Perhaps a hen cackles to inform other hens that she is occupying a localized area. Those females which cackled and whose status were known did so when they were settled on a restricted area. Since hens answer other hens and often

approach the sound, or make themselves more conspicuous, an information system among hens, rather than between hens and cocks, seems the most likely option.

Why would a hen advertise her presence to another female? She is not attracting a hen to her; although some hens approach, (likely in response to a call given on part of her home range), they rarely encounter her. Radio-tagged hens were sighted near other hens on only a few occasions. Spontaneous cackles often go unanswered. The most obvious alternative is that this call warns other hens to stay away. Hence, hens may be spacing themselves by mutual avoidance, a mechanism proposed for female spruce grouse (Herzog 1977).

If the function of the cackle is to space hens on the breeding range, thus helping to determine their numbers, what is the adaptive significance of spacing? Spacing may ensure an adequate food supply in the pre-nesting or incubation periods, allow maximum dispersion of nests lessening predation on eggs, or guarantee food, area, and cover for broods. My study presents no data to support any of these hypotheses and more detailed experimental work is required to test the above possibilities.

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Table 1. Age, date of capture, calcium level, date of laying first eggs and behavioral ratings of radio-tagged hens, 1977.

Hen No.	Age	Capture date	Calcium (ppm)	First egg date	Behavior rating
67	Y	4 April	110	15 May	4
65	Y	9 April	110	22 May	1
55	Y	11 April	100	24 May	2
64	Y	11 April	110	18 May	2
93	A	9 April	120	30 April	3
79	A	10 April	125	16 May	2
95	A	11 April	185	9 May	5
80	A	15 April	160	7 May	2
81	A	15 April	?	17 May	2

Y=Yearling, A=Adult.

Table 2. Duration of localization of radio-tagged hens before laying first eggs.

	Number of days localized prior to laying first egg								
	Yearlings				Adults				
Hen No.	67	65	55	64	93	79	95	80	81
	11-13	13-16	13-15	11	6	5	23	20	8

Table 3. Distance (km) from capture site to nest site of radio-tagged hens.

Yearlings		Adults	
Hen No.	Distance	Hen No.	Distance
67	1.07	93	0.19
65	1.05	79	0.63
55	0.18	95	0.46
64	3.00	80	0.095
		81	0.41
$\bar{X}\pm SE$	1.33±0.59		0.36±0.08

Table 4. Size of home ranges (ha) of pre-nesting hens, (number of locations in parentheses).

Hen No.	Total		After 15 April		20 days prelaying	
			YEARLINGS			
67	31.14	(26)	14.94	(20)	8.56	(16)
65	26.67	(24)	20.23	(19)	8.92	(13)
55	12.44	(26)	13.18	(23)	1.31	(13)
64	18.55	(17)	18.08	(14)	4.35	(9)
$\bar{X}\pm SE$	22.22±4.16		16.61±1.57		5.79±1.81	
			ADULTS			
93	2.20	(12)	0.54	(10)	2.20	(12)
79	21.27	(23)	18.71	(20)	4.31	(14)
95	5.75	(19)	3.55	(17)	1.93	(14)
80	3.57	(18)	3.57	(18)	3.40	(16)
81	4.99	(16)	4.99	(16)	1.76	(12)
$\bar{X}\pm SE$	7.56±3.48		6.27±3.19		2.72±0.48	

Table 5. Age, calcium levels, and reproductive classification of hens which cackled and were then captured.

Date	Band No.	Age	Calcium (ppm)	Reproductive Classification
		1976		
12 May	11158	Yearling	320	B
15 May	11236	Yearling	?	B
		1977		
5 May	11519	Adult	240	B
7 May	11523	Yearling	360	B
19 May	11634	Yearling	390	B
7 May	11524	Adult	?	?
10 May	11525	Adult	?	C
		Radio-tagged hens 1977		
26 April	#81	Adult	-	A
16 May	#65	Yearling	-	B

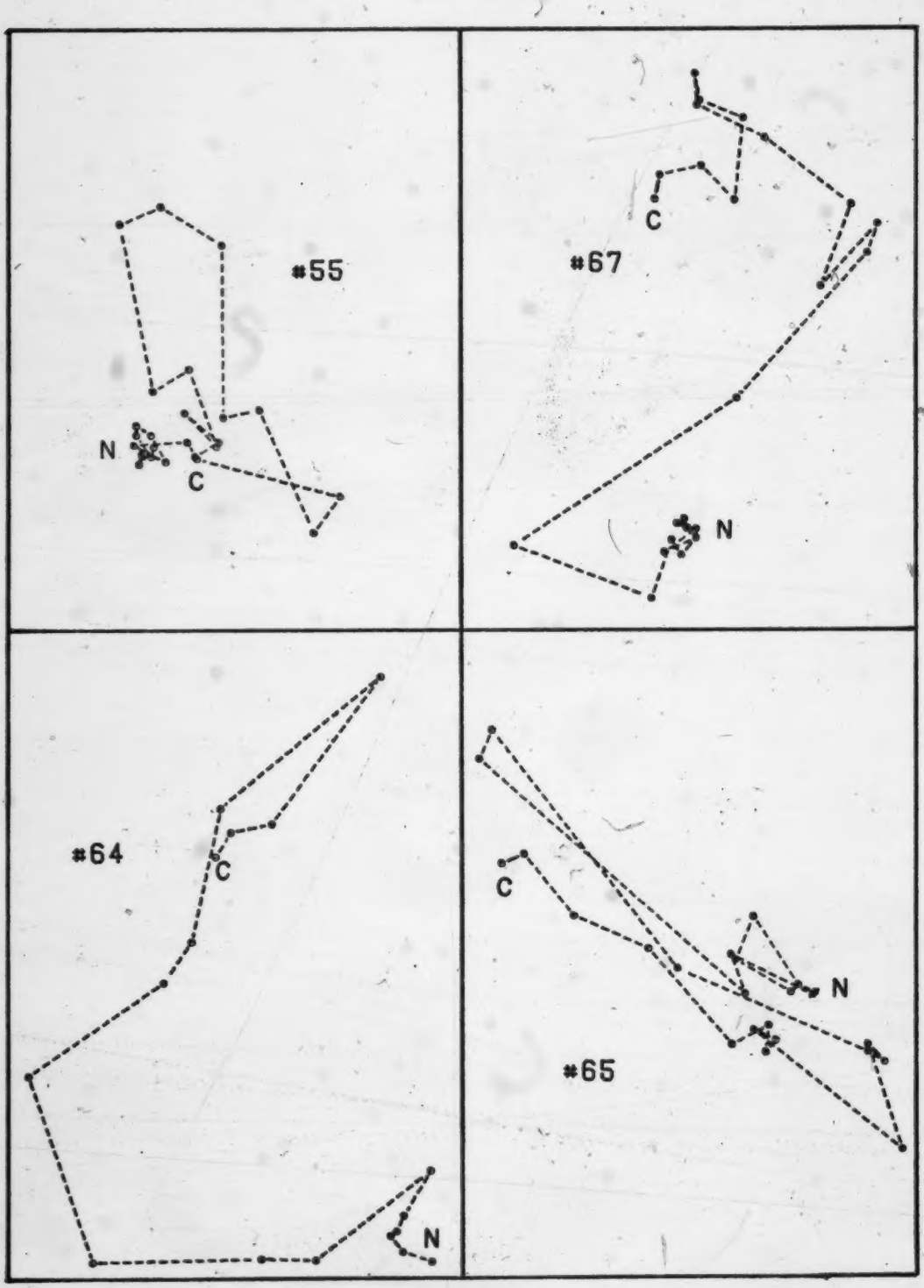

Figure 1. Movement patterns of yearling pre-nesting hens, 1977 (C=capture site, N=nest site, scale (55,67,65): 1 cm=218 m; (64) 1 cm=436 m).

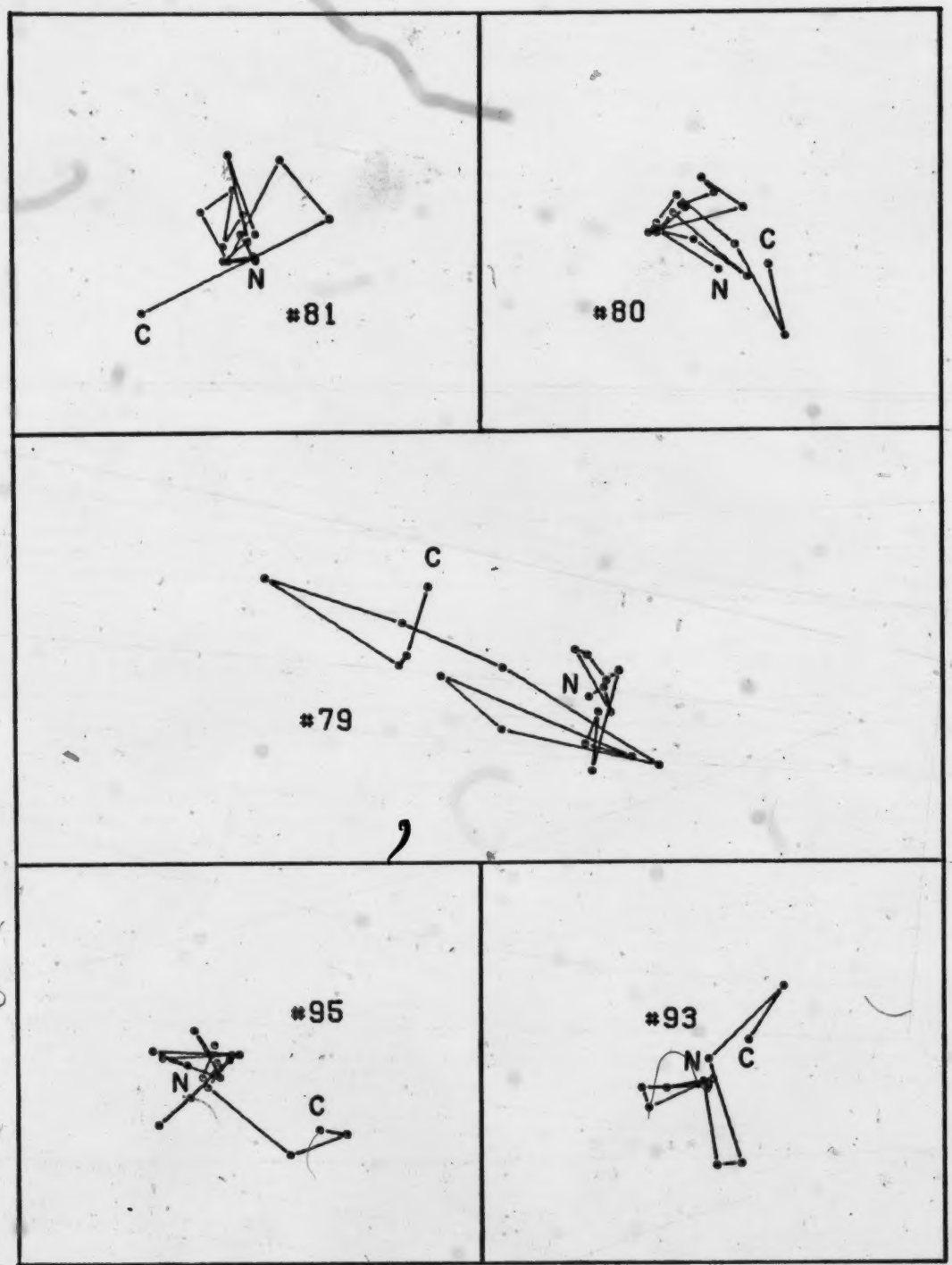

Figure 2. Movement patterns of pre-nesting adult hens, 1977 (C=capture site, N=nest site, scale: 1 cm=218 m).

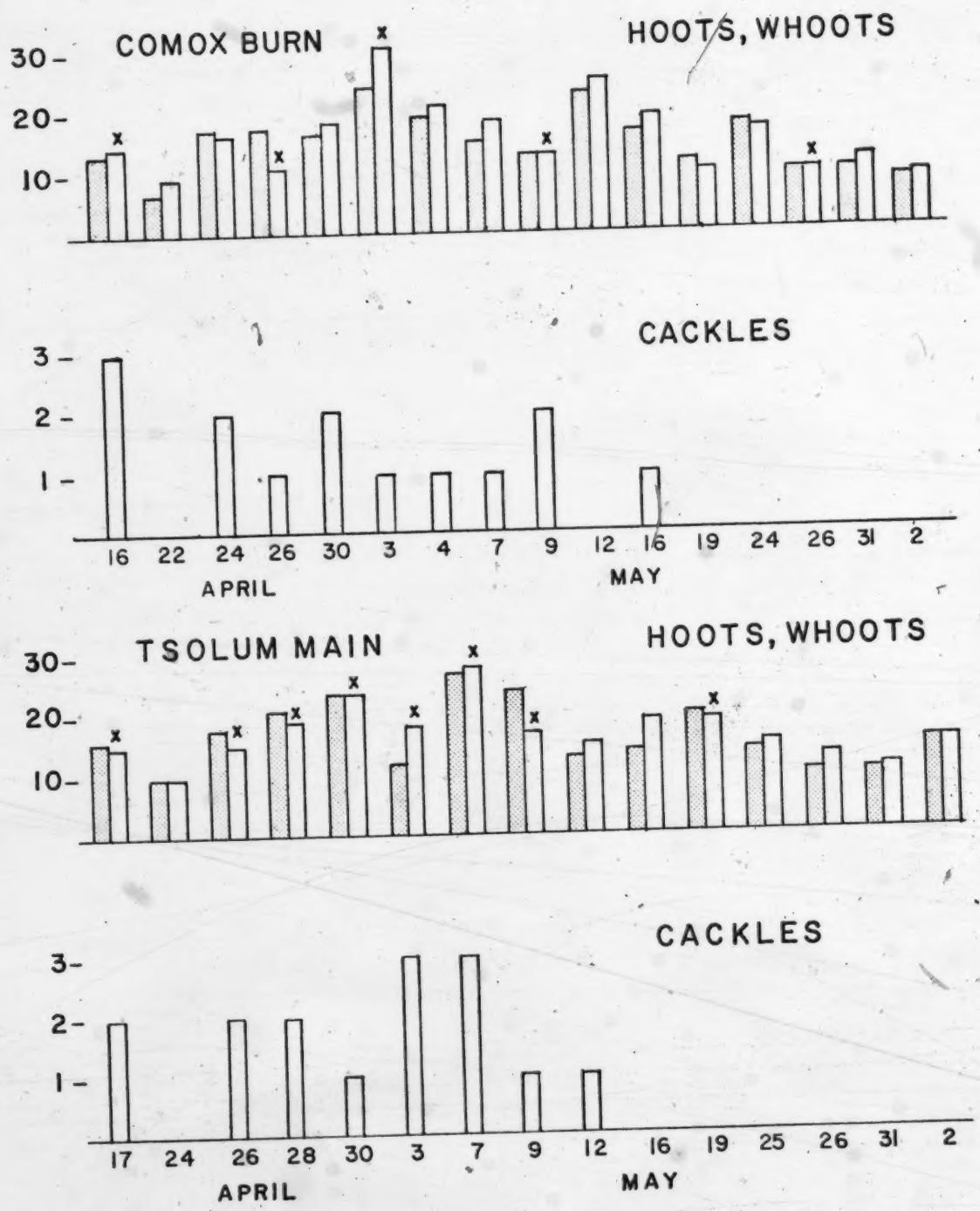

Figure 3. Incidence of hooting, whooting, and cackling during cackle transects, 1977 (mean hoots before tape played shaded, mean hoots after tape unshaded, X denotes whooting heard).

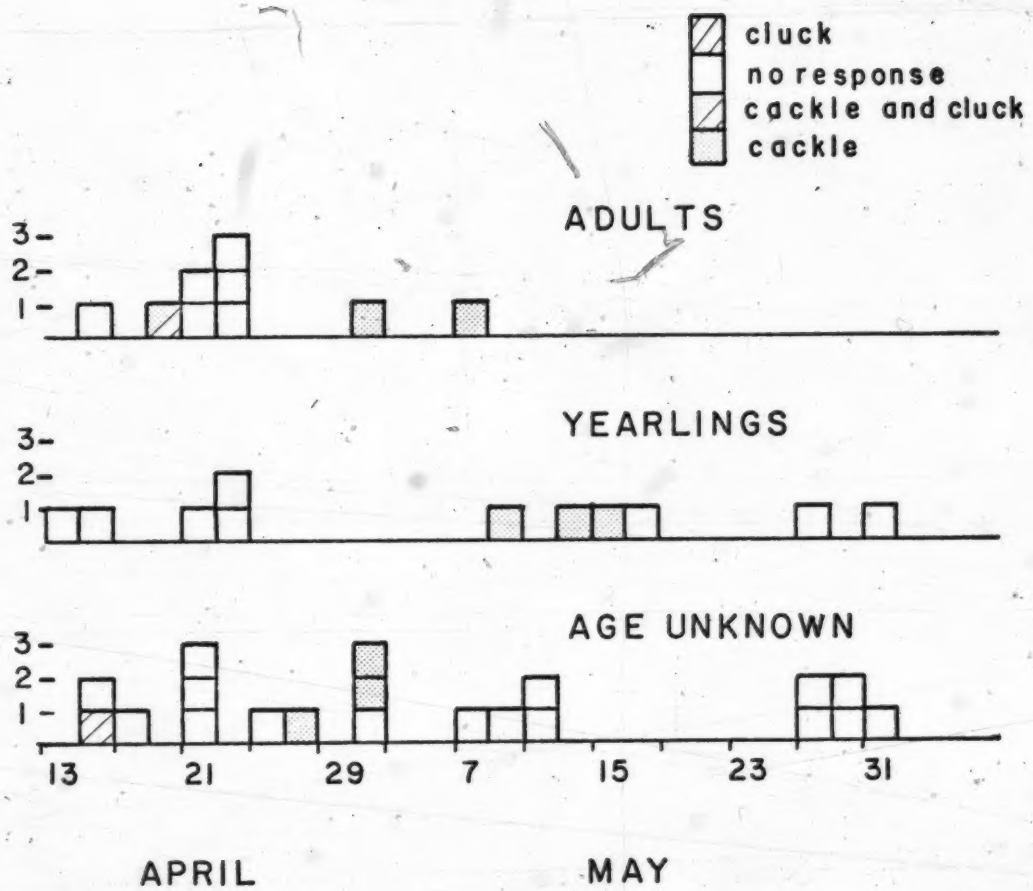

Figure 4. Vocal responses of non-radio-tagged hens during individual cackle experiments, 2 day periods combined.

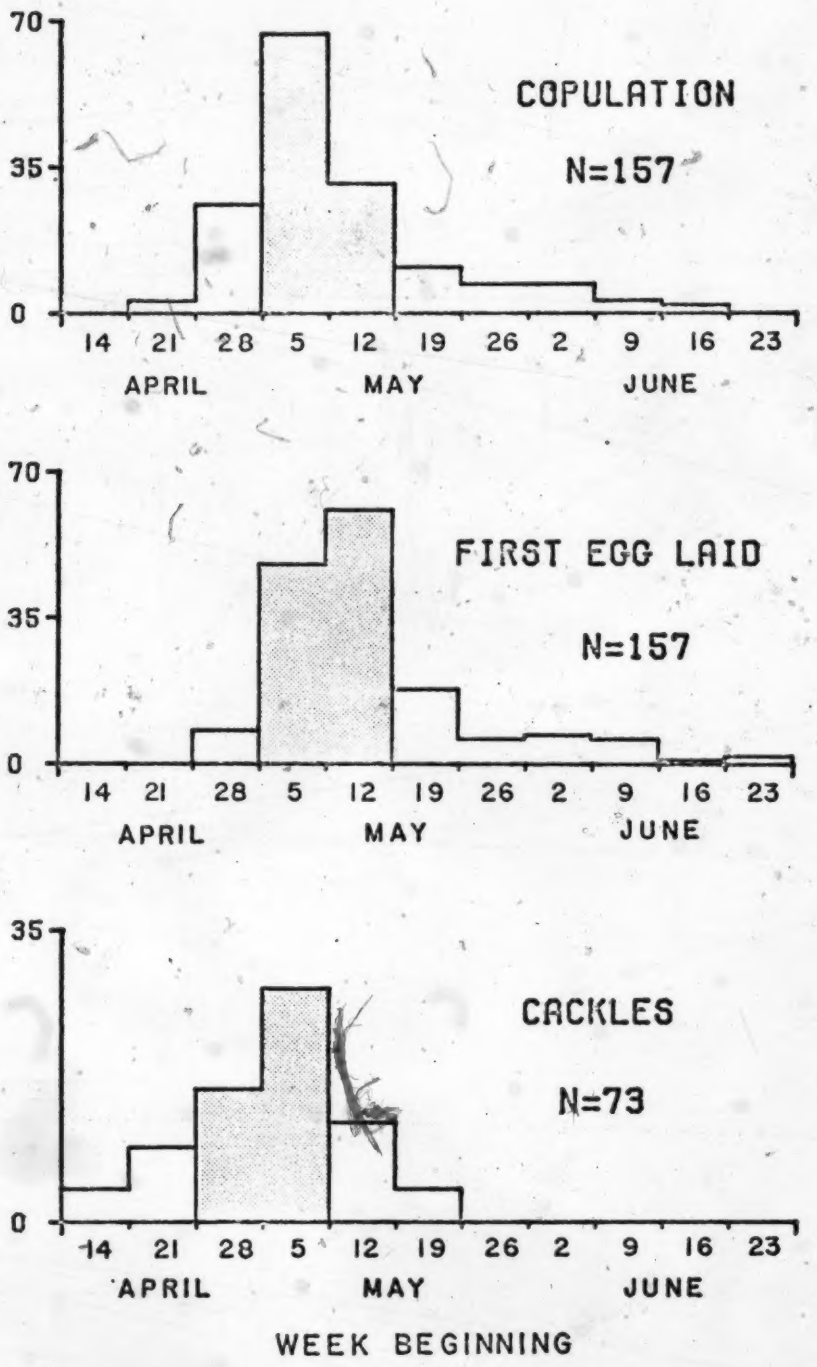

Figure 5. Comparison of the incidence of cackling to timing of copulations and dates when first eggs were laid, data from 1976 and 1977 combined. Peak periods are shaded.

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THESIS DISCUSSION

Two general theories on how populations are regulated have been proposed. Exponents of the "extrinsic" school of thought, notably Lack (1954,1966) propose that mortality, caused by starvation or other factors outside the animal, controls density. Although realizing that extrinsic factors may vary numbers somewhat, proponents of the "intrinsic" school suggest that factors inside the animal, such as behavior, endocrine levels, or genetic characteristics are most important in determining numbers (Wynne-Edwards 1962, Christian and Davis 1964, Chitty 1967, see Watson 1973 for review).

Zwickel and Bendell (1972) compared three populations of blue grouse at different densities and concluded that extrinsic factors such as structure of vegetation, quantity and quality of food, weather, disease, parasites and predation may set broad limits to population increase, but that intrinsic mechanisms were likely important in determining numbers.

An important distinction must be made between the mechanism of regulation and the ultimate factor to which the mechanism sets the density. In other words, the same mechanism may stabilize density at two different levels in two areas. Much of the recent research on blue grouse has

been primarily aimed at determining the mechanism of regulation. Factors such as early mortality of young and mortality of established breeders (Zwickel and Bendell 1967), clutch size, fertility and hatchability of eggs, and nesting success (Zwickel 1975) bore no relation to recruitment the next spring.

Removal experiments indicated that "surplus" yearlings existed which recolonized vacant areas in spring (Bendell et al. 1972, Zwickel 1972). These studies indicated that social interaction was important in regulating the number of yearlings which recruited.

The importance of territorial or aggressive behavior in males in determining spacing and breeding density has been discussed (Wynne-Edwards 1962, Tompa 1962, Jenkins et al. 1967, Bendell and Elliott 1967, Krebs 1971). The role of the female has been largely ignored or dismissed.

I examined two main questions:

1. Is behavior of females important in determining spring breeding density?
2. Can females which recruit be distinguished from those which will not?

Herzog and Boag (1977), in a recent study on spruce grouse, reported that hens occupy territories which are aggressively defended throughout early spring and during nesting. They suggested that aggressive behavior of hens influenced numbers by spacing females and causing spring

dispersal of yearling hens.

Aggressive interactions among females have been reported in other species of tetraonids such as sage grouse, Centrocercus urophasianus, (Lumsden 1968), black grouse, Lyrurus tetrix, (Kruijt and Hogan 1967), greater prairie chickens, Tympanachus cupido pinnatus, (Robel 1970, Robel and Ballard 1974) and red grouse, Lagopus lagopus scoticus, (Watson and Moss 1971). In the lekking species, dominant females have been observed to delay or prevent submissive females from breeding. Delays in, or complete inhibition of, breeding in subordinate females have been noted in other species (blackbirds (Crawford 1977), magpies, Gymnorhina tibicen, (Carrick 1963) and rodents (Christian 1971)). Thus aggression among females may be more common than was once thought.

My data indicate that adult female blue grouse may delay, or in some cases completely suppress, breeding activity of yearling females, by actively advertising their presence on a localized area. Once yearlings have localized, they likely interact with non-localized yearlings. Spacing appears to develop through mutual avoidance, with potential recruits avoiding resident adult or yearling hens. Site attachment or localization appears to be an important criteria for initiation of gonadal recrudescence. Yearlings which do not settle, do not breed, and can be considered "surplus" to the breeding population.

Non-breeders are present on the area until yearlings

have begun to lay. This implies that exclusion is not a rapid process occurring before peak breeding, but rather that a group of yearlings wanders over the available habitat looking for a place to settle. Those that do not localize, leave. The sudden disappearance of non-breeders after laying begins in breeding yearlings, may indicate that it has become physiologically impossible for some yearlings to breed.

Can recruited yearlings be distinguished from "surplus" yearlings? Zwickel et al. (1978) compared birds colonizing a removal area to those recruiting into an established population and found no evidence for intrinsic differences between the two groups. I found that breeders weighed more than non-breeders.

My data suggested the following model for regulation of female density in spring (Fig. 1). The pattern of recruitment illustrated here is supported by the distribution of laying in yearling hens: few lay early and the bulk lay after most adults are incubating.

The model could be further tested by removing all adults from an area. If adults suppress yearlings, yearlings on the removal area should localize and breed earlier than those on a control area. Factors such as aggressive behavior, body weight and condition could be compared between recruits on each area.

If females are regulating their own numbers, how is the density of males determined? Since sex ratio is equal

(Zwickel and Bendell 1967), a relationship between the mechanisms for female and male regulation is implied. Zwickel (1972) suggested that breeding density may be set by females, with the number of yearling males adjusted to the total number of females. Obviously more emphasis should be placed on studying the behavior of yearling males, and their interactions, if any, with females. One-sex removal experiments could test whether the sexes are regulating their densities independently.

I feel this study emphasizes the need for observing female behavior in the field. The probable importance of female behavior in population regulation has been voiced by others (Tompa 1962, Myers and Krebs 1971, Zwickel 1972) but, with few exceptions, little has been published on the subject. The secretive nature and rapidly changing reproductive status of females of some species complicate study. An understanding of female reproductive physiology and the use of methods such as radio telemetry will help to surmount some of the difficulties.

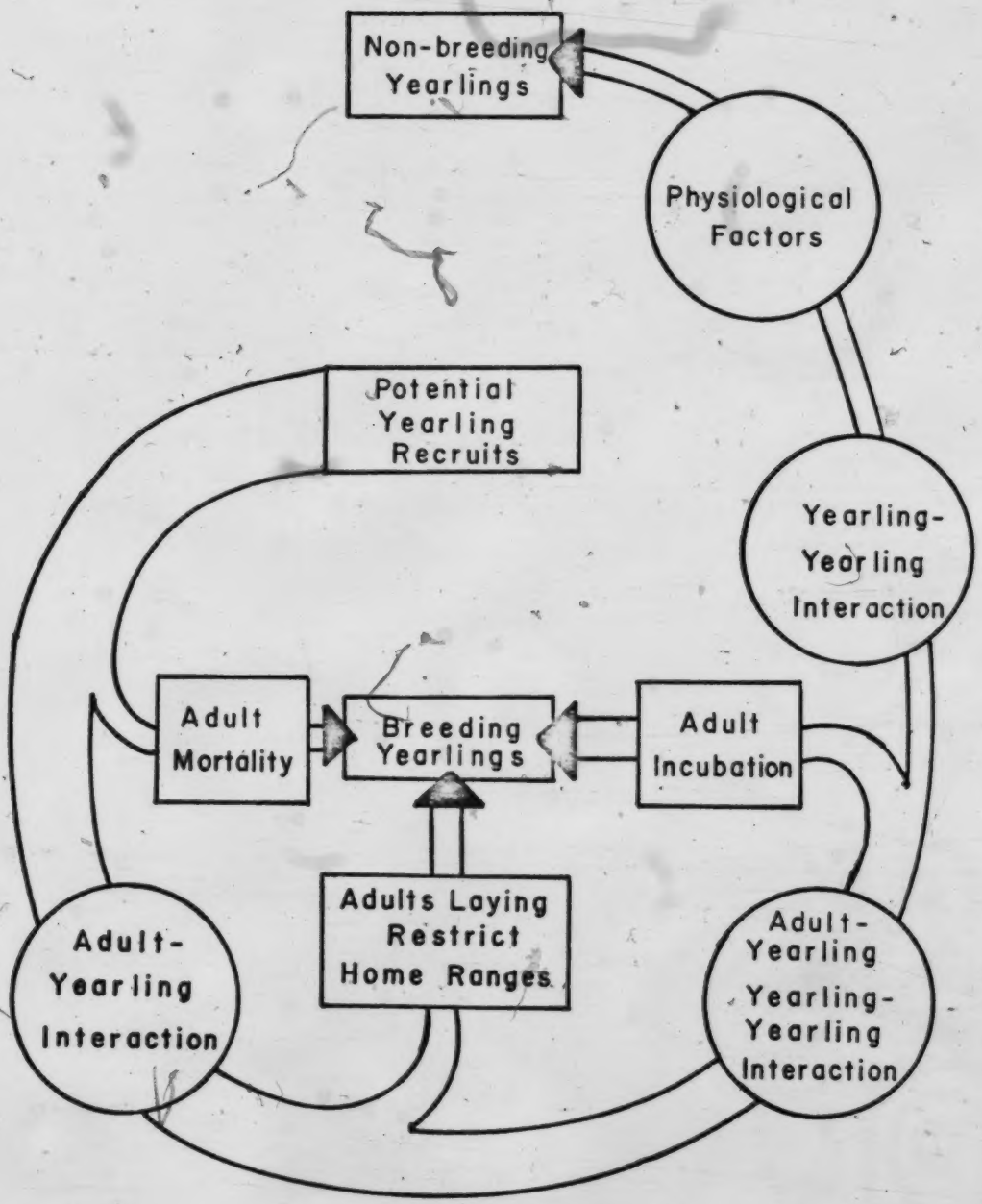

Figure 1. Model of the pattern of yearling female recruitment in spring. Size of arrows denotes proportion of yearlings, circled items denote factors inhibiting yearling recruitment, and items on arrows denote factors favoring yearling recruitment.

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Appendix 2: Incidents in which the cackle or whinny was heard.

Incident 1. 9 May 1975, 1500, Comox Burn
As I approached a hooting male, a hen cackled. The male moved toward the female in courtship display and whooted. I played the cackle tape and the female cackled back. She hopped onto a stump and looked around alertly while calling. The cock ran around the base of the stump in display and whooted again. The female continued cackling, and the male moved away and began to hoot. This hen vocalized for about 10 minutes.

Incident 2: 20 April 1976, 1310, Comox Burn
I discovered my dog in a depression pointing an unbanded male which appeared to be a yearling. The male flushed. The dog suddenly pointed again, 3 m away from where the male had been. I circled a dense fir copse 2 m upslope from a small stream, but could not see a bird. A soft cluckling emanated from the copse. The dog and I withdrew across the stream and the female model was set in the open on a stump. We hid behind some trees about 6 m away and waited in silence for 15 minutes. As soon as the taped cackle began, the hen responded with a soft cackle, after each cackle in the tape, for 70 seconds, and then remained silent. We approached and found the hen standing on a log about 20 m to the south of her former position, pointed away from the source of the tape. She was a banded adult (3854) and was quite tame. I clucked at her and she clucked softly, looking alert with crest raised and tail up. She flushed over a ridge to the southeast.

Incident 3: 1 May 1976, 1330, Comox Burn
I found my dog pointing into a thicket and sighted an unbanded hen standing on a log. I set the dummy on a log in a clearing nearby, withdrew to hide, and waited 15 minutes. As soon as the cackle tape started the hen cackled back, for about 20 seconds , after each call on the tape. I crept around and saw her at her former position. She walked away from me and towards the model, cackling softly, hopped up on a log, crest raised, and looked around. Backing off, I placed the model in her view and played the tape. The hen cackled five more times. She flew away clucking when I attempted to noose her.

Incident 4: 2 May 1976, 1620, buffer area
I had been playing the tape on a male's territory when

I heard two cackles, in the distance. I approached the area and played the tape again and the hen answered. As I approached more closely, the hen did not respond to the tape and could not be found.

Incident 5: 9 May 1976, 1000, Comox Burn
My dog pointed into dense plantation on a slope close to a small stream surrounded by willow (Salix sp). The trees were very dense and I could not see the bird. I withdrew 10 m and conducted an experiment. When I began to play the tape, 15 minutes later, a hen cackled back for 60 seconds after each call on the tape . A male began to hoot on the ridge above us. The hen did not respond further but I saw her crouched between two trees. She stood and began to walk leisurely upslope, pecking at the ground. She was a banded adult and walked out of sight over the ridge.

Incident 6: 12 May 1976, 1445, buffer area
My dog followed a circular trail on a steep slope. I walked upslope and saw a hen running. We concealed ourselves and waited 15 minutes. The hen responded immediately to the tape and cackled after each call for 60 seconds, then ceased. She was in the same position where I had first sighted her, but flushed south 50 m. I followed as she ran, clucking, with crest and tail raised. After a long chase I noosed her. She was yearling female 11158 and was fitted with a radio transmitter. She did not nest but ranged widely over the area.

Incident 7: 15 May 1976, 1230, buffer area
My dog flushed a cock on a flat area at the base of a ridge. As I walked to where he had been, an unbanded hen flushed 10 m and landed clucking with crest erect. She then flew east 100 m to the ridge top. A second male flushed from 15 m away from where the hen had been. I approached the ridge where the hen landed, hid, and waited 15 minutes. As soon as the tape began, the hen responded to each cackle for a minute then stopped. I heard several whoots and saw a cock in display on a log, with the hen running down the log. The male moved off and hooted. I found the female crouched on a log nearby and captured her. She was yearling female 11236. A radio was affixed to her and she laid her first egg 23 May.

Incident 8: 21 April 1977, 0940, Comox Burn
I was testing radio-tagged hen #67 with the cackle tape. She did not respond but another hen answered 4 times from the north about 100 m. Several whoots were heard from that direction and the cackles ceased. I did not locate the hen.

Incident 9: 26 April 1977, 1450, buffer area
Radio-tagged hen #81 was found on a ridge in dense

plantation by triangulation. I hid about 20 m away and waited 20 minutes in silence. After the first 3 cackles on the tape, the hen responded from above me and cackled softly 8 times. Suddenly a cock landed about 10 m from me and began hooting . The hen ceased cackling. When the tape was finished, I approached the spot where the cackling had been heard and found #81 standing in some trees.

Incident 10: 26 April 1977, 2100. Tsolum Main

At the last station of the cackle transect a hen responded frequently. After the transect was finished I approached her and played the tape . She immediately cackled back. A male flew in and began to whoot. The female continued calling. I left the tape playing and approached the area. The hen flew 15 m, followed by the male , then flew out of sight. I returned to collect the tape recorder and heard cackling and several "whinnies". As I drew near, the vocalizations stopped. I played a few cackles on the tape. A hen clucked in a 3 m tree about 10 m away and a second whinnied from under the tree. This continued for about a minute. The hen in the tree suddenly flew, giving 2 high pitched "shriek whinnies". The second female clucked a few times and then flushed in the same direction, giving two "shriek whinnies".

Incident 12: 29 April 1977, 1935, buffer area

My dog trailed in a mixed conifer thicket beside a logging road and eventually pointed up a slight slope. I saw an unbanded hen crouched in the open on the slope. We hid behind a tree about 15 m away and waited in silence. When the tape began, the hen cackled, usually after each call on the tape, but sometimes she strung 2 together. The cackles began softly but grew louder. She cackled 10 times. While vocalizing she rose from a crouch and looked around. A cock flew onto the road behind me and hooted but did not approach the hen. I attempted to noose the hen, but she was very wary and began to cluck, looked around in an alert posture, walked a few steps, then flushed.

Incident 13: 1 May 1977, 2045, buffer area

The cackle tape was played during an experiment with radio-tagged hen #79. After the first taped call, a hen flew in from the southeast, cackling, and landed in a 10 m tree about 15 m from the tape recorder. Upon landing she cackled once and gave one low pitched whinny. Immediately, a cock flew into the tree, missed a branch, and landed on the ground. The female flew towards the recorder, cackled and landed about 10 m in front of it. The cock followed in full display and hooted. The female remained silent. I attempted to noose her but she flushed.

Incident 14: 2 May 1977, 0945, buffer area

I was waiting the usual 20 minutes before beginning a

cackle experiment with radio-tagged hen #55. Five minutes before I started the tape, a female spontaneously cackled from about 30 m north of me and about 50 m north of #55. She called for about 30 seconds, waited 30 seconds and called 3 more times. No other hens responded . When the tape began she immediately cackled and "whinnied". She cackled 35 times and "whinnied" 12 times very loudly. She continued vocalizing after the tape was completed. I found her crouched on a log. During the tape a male performed a flutter flight behind me and began to hoot, but did not approach the hen.

Incident 15: 2 May 1977, 1120, Comox Burn

I was driving along a logging road on a motor bike when I saw an unbanded hen run from the side of the road up the slope at the edge. I hid across the road behind a tree. At 1135 she shook her feathers twice. At 1140 I played the tape and immediately another hen to the south cackled 6 times. The hen across the road cackled once but remained stationary. I noosed her after the experiment and found she was an adult, 11518. While banding her, I heard a hen cackle to the south 3 times.

Incident 16: 2 May 1977, 1320, buffer area

The tape was being played during an experiment with radio-tagged hen #95. In the distance I heard a faint cackling which became louder as the hen approached. Hen #95 gave a few short soft clucks, then was silent. The other hen approached to within 60 m of the tape, still calling. I sighted her across a clearing on a large log. A male in full display followed her along the log, but the hen ignored him and continued cackling. The cock left. I approached the hen and attempted to catch her but she ran off . She was tame, but was very wary of the noose and I spent a futile one and a half hours chasing her.

Incident 17: 2 May 1977, 1620, buffer area

During an experiment another female cackled about 20 m from #67. She responded immediately after the first call on the tape, with 3 very long cackles, then responded after each cackle on the tape. Her call was louder as she approached. She cackled loudly 38 times during the tape. When the tape finished, I circled and tried to noose the hen that had vocalized, but flushed her. I then flushed a third hen from about 2 m from #67.

Incident 18: 5 May 1977, 1010, buffer area

A female model was set on a stump and I hid behind a tree and waited a few minutes in silence and played the tape. A hen answered on the third call and gave 13 cackles. About a minute later I heard a male whooting from the same direction. As I approached a male ran off in full display and I flushed a hen.

Incident 19: 5 May 1977, 1945, buffer area
My dog and I were hidden and I played the tape. A female answered, to the west, cackle for cackle on the tape, 13 times, then stopped. The dog and I approached , but the dog flushed the hen.

Incident 20: 5 May 1977, 2110, Comox Burn
I set a female model along a bank at the road's edge and played the cackle tape. A male immediately made a flutter flight onto the road 20 m below me and began to hoot. After several calls on the tape, a hen across the road cackled loudly 5 times. The male flew and landed on loud wing near the sound. She became silent. The dog and I searched for the hen and the male was found on stump. I saw the hen sitting on a 3 m tall tree in a small bog. I captured her and found she was an adult, 11519.

Incident 21: 7 May 1977, 1030, buffer area
I had just finished an experiment with radio-tagged hen #55 when a hen cackled 3 times to the north. I played the tape again and heard cackles from the east 25-30 m away. Approaching , I saw an unbanded hen standing on a log. I noosed her. She was yearling 11523 and was fitted with a radio transmitter. She laid her first egg either that day or the next.

Incident 22: 7 May 1977, 1920. above Tsolum Main
A female model was placed on a log and I hid behind a tree. As the tape started, a cock made a flutter flight to the area, hopped onto a stump and hooted 2 m from the dummy. A female across a nearby logging road to the south, about 50 m away, cackled after each call on the tape. When the tape stopped, a second hen cackled below me to the north. The two hens vocalized together, then I heard whooting coming from near the second female. The dog and I searched for the first female. The dog picked up a trail above where the vocalizations had been heard, trailed downslope towards the tape and pointed into some willows. I circled and sighted a hen on the ground near a rotten stump. She flew across the road clucking. We followed but she flushed again. We proceeded to where we had heard cackling from the second hen. The dog soon pointed. I circled and a hen flushed upslope and landed on a log, clucking. I noosed her (adult hen, 11524). We searched again and flushed another hen from some willows downslope.

Incident 23: 8 May 1977, 0840, Tsolum Main
It was a cold windy morning and I had been playing the cackle tape from 0605 with no response. At 0840 I hid behind a tree and started the tape. I heard a hen answer the first 7 cackles in the tape very faintly to the southeast and then stop. I could not pinpoint the source of the sound and she did not respond further to the tape.

Incident 24: 10 May 1977, 0645, buffer area

My dog and I hid in the bushes along the edge of a road and I played the tape. Immediately a female answered from the west on the slope above us. She cackled 7 times, to every second call on the tape, then stopped. The dog and I approached and the dog picked up a trail and pointed into some willows. I circled and saw a hen crouched on the end of a log which was protruding about 1.5 m above the ground. I captured her (adult hen, 11525) but the dog continued trailing and pointed onto a ridge 3 m away. I heard running and saw a banded male in display run into a thicket. This cock was probably the bird the dog had initially been trailing. The hen was about 100 m northwest of the tape. She had a full brood patch. The dog and I searched for more females. We found one about 100 m to the southwest. She flew out of sight clucking.

Incident 25: 16 May 1977, 1630, buffer area

I located radio-tagged adult #80 on her nest on the west side of a creek when I heard a spontaneous cackle from the east side of the creek. I played my tape and heard an immediate and long response from across the river. On crossing the creek I played the tape again but heard no response. I searched for 20 minutes but could not see the hen. Then I listened for #65's signal on my receiver and found her walking along the ridge from where the cackle had been given. No other hens were seen in the area. Yearling #65 had cackled on #80's pre-nesting home range, but #80, on her nest across the creek, did not reply. #65 laid her first egg 6 days later at the spot where she had been vocalizing.

Incident 26: 19 May 1977, 2130, Upper Tsolum Main

I sighted a hen at the edge of a logging road. She hopped onto a small log, crest raised, then ran. I withdrew 15 m and waited 10 minutes in silence. As soon as the tape began, she cackled long calls, fairly loudly, 4 times. A male made a flutter flight to the area and the hen stopped calling. I saw the cock in full display on a log to the west. I circled and found the hen standing on a log about 10 m from where I had hidden. She was captured (yearling hen, 11634).

Incident 27: 29 May 1977, 1220

This incident occurred in an area of mature timber close to the ocean about 16 km east of the study area. A hen was sighted crouched at the edge of a road. Simulated chick distress whistles were given by two observers. The hen walked across the road, crest raised, into the vegetation. She gave 3 or 4 "whinnies", then flew into a tree. A second female was seen 100 m further down the road. She responded to a simulated chick whistle with a "gaw-gaw" sound, "whinnied" loudly several times, and flew into a tree.

Summary of whinny responses

Whinny-like calls were heard infrequently and in a variety of circumstances. It is doubtful whether each was exactly the same, but all "whinnies" were given in agonistic encounters or situations. I heard 3 types of "whinnies": a muted whinny given by females in interactions with other hens (incidents 10,13,14, App. 3, expt. 11); a "shriek whinny" given by hens in what appeared to be fearful or painful situations (incident 10, App. 3, expt 13) and a "gaw whinny" also given in aggressive or agonistic interactions (incident 27). Precopulatory whinnies, as described by Stirling and Bendell (1970), were not heard.

Appendix 3: Experiments with incubating hens.

Methods

Several experiments were performed on incubating hens to determine if they were aggressive at their nest site. While the hen was on the nest, a female mounted in neutral posture was extended on a pole by a hidden observer to within 1 m of the nest for 2 minutes. A second experiment used a brown shoe box mounted on a pole as a control. The third type involved erecting a blind 5-10 m from the nest and waiting until the hen left the nest to feed. Either a female mounted in the neutral posture or a live hen in a round plexiglass cage was placed beside the nest and the observer hid in the blind and waited for the hen to return.

Results

Five hens were experimented with in 1976, but each was not tested to the same extent. These experiments indicated that some hens are aggressive to other hens at the nest site, but there is a great variety of response.

Experiment 1: 5 June 1976, 1020, nest 76-5 (Yearling)
Fifteen minutes after arriving at the nest a female model was extended towards the nest on a pole. The hen flushed to a group of logs about 10 m away and clucked 5 or 6 times. Her crest was raised and her combs were visible. She disappeared and I left.

Experiment 2: 5 June 1976, 1138, nest 76-29
After concealing myself in some bushes, I moved a female model on a pole towards the nest. When it was 60 cm from the nest, the hen did not move. When the model approached to 30 cm, she flushed 10 m away, clucking.

Experiment 3: 7 June 1976, 2130, nest 76-27
A large tent blind had been erected 7 m from the nest. At 2130 I entered the blind and observed the hen's behavior through a spotting scope. At 2146 she turned her head from side to side for about 20 seconds then stood, walked away and flew east. At 2202 I heard flight noise and the hen landed about 10 m from the nest site, stood for 5 seconds looking around, walked towards the nest, jumped onto a large log, then jumped down in front of the nest and walked on. She settled herself but did not appear to turn the eggs. I watched until it grew dark, then slept in the blind. At 0400 she was on the nest, at 0430, she flew to the east. I set up a female dummy about 20 cm from the nest. At 0450 the hen flew to about 3 m in front of the blind. A male flew in from the west almost simultaneously and landed on the road 10 m from the blind. The hen gave a very soft series of 5 "liquid clucks" (J. Kristensen, unpublished data) and walked onto the nest past the model. The male approached the dummy in full display, head bobbing, stopped on a log, head bobbed, approached the model , stopped in front of it and pecked it about 10 times. He mounted the model, grasped the feathers at the nape of the neck and attempted copulation. He dismounted when the model fell over and moved towards the incubating hen. He moved to the back, to the front, and to the back of the nest giving a whoot each time. The nest hen remained motionless. The cock hopped onto the log covering the nest, head bobbing, still in display, then walked towards the blind. At 0530 he proceeded down the road to the west in full display, pecking at the ground and left my view.

Experiment 4: 8 June 1976, 0907, nest 76-34
A small teepee blind was set up the night before. At 0921 I advanced a female model on a pole towards the nest. When the dummy was about 2 m from the nest, the hen walked off clucking, stopped on a log about 2 m away, clucked, then walked off clucking and stood 15 m from the nest. She did not raise her crest or combs .

Experiment 5: 11 June 1976, 1010, nest 76-27
One observer sat in the tent blind, while I advanced a female dummy on a pole to within 30 cm of the nest. The hen jumped off to the west over the slope and I could not see her. About 2 minutes later I heard a very soft "liquid cluck", then the hen approached the

dummy and pecked its head about 20 times, then struck the head with her wing. She stood beside the model for 20 seconds, then pecked 25 more times , bumped the model in the chest with her body, then ran around the model and onto her nest.

Experiment 6: 12 June 1976, 1130, nest 76-32
A teepee blind was erected 7 m to the west of the nest. I was in the blind and an assistant hid behind a tree 5 m away. After 10 minutes he extended the female model on the pole to 2 m from the nest. The hen did not respond. The model was moved to within 30 cm and the hen ran off and flew away.

Experiment 7: 12 June 1976, 1500, nest 76-5
A cardboard box on a pole was extended to the nest by a hidden observer. When the box was 30 cm from her, the hen jumped off and ran to the north, clucking 3 times.

Experiment 8: 13 June 1976, 2030, nest 76-5
At 2030 I arrived at the nest and set up a teepee blind 5 m to the east of the nest. At 2139 I heard the hen fly off, so I placed a female dummy 60 cm in front of the nest and returned to the blind. At 2156, the hen flew in from the west and landed 10 m from the dummy. She walked towards the nest . She flew on top of the log under which the nest was located and clucked twice, then jumped down. She began to "liquid cluck" 30 cm from the dummy, walking back and forth in front of it. At 2204 she stopped clucking and disappeared behind the log. I removed the model as it was getting dark.

Experiment 9: 14 June 1976, 1150, nest 76-29
One observer hid behind a stump to the west of the nest, and I hid behind a tree to the east. At 1200 I advanced a cardboard box to within 1 m of the nest but no response occurred. I advanced the box another 90 cm. She jumped up and ran clucking, five times, about 3 m to the south, drooping her primaries and hissing. She ran around behind me, primaries drooped to the ground. She then stood about 3 m from the nest, drooping her primaries. She head bobbed and clucked for about 5 minutes. I withdrew the box and left.

Experiment 10 14 June 1976, 1335, nest 76-27
One observer sat in the tent blind while I hid close to the nest. We waited in silence for 10 minutes and then extended the box to within 50 cm of the nest. The hen looked at it but did not respond. The box was removed.

Experiment 11: 16 June 1976, 2135, nest 76-27

I placed a live female in a plexiglass arena in front of the nest. The hen in the arena began to cluck. The incubating hen jumped up and wing struck the cage 7 times, tail fanned, then pecked at the cage. She gave a soft "whinny" 4 times during the attack. Then she hopped back onto the nest.

Experiment 12: 17 June 1976, 2050, nest 76-32

The live hen in the arena was placed close to the nest . She started clucking. The incubating hen jumped up and began to cluck. The caged hen continued clucking and the 2 hens clucked together for about 4 minutes. Then the incubating hen moved away so the caged hen was removed.

Experiment 13: 17 June, 2135, nest 76-29

The caged hen was placed 30 cm from the nest. The hen was away feeding. I hid behind a tree 3 m to the east. At 2135 the hen returned from feeding. She flew in from the north and landed 7 m from the nest, then walked onto it. The caged hen was clucking, but the nest hen walked by her with no apparent response. I removed the cage and left. When I removed the hen from the cage she gave a loud "shriek whinny" and I noticed that her leg was broken.